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FUNCTIONAL ANATOMY OF THE VERTEBRATES

BY

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FUNCTIONAL ANATOMY OF THE VERTEBRATES

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This book is dedicated to the memory of George W. Crile and Grace McBride Crile. Dr. Crile, surgeon, research worker, and author, possessed among his natural endowments the gift of insatiable intellectual curiosity which compelled him to constant search for an explanation of the processes activating living phenomena. Mrs. Crile, devoted to the studies of her husband, and faithful chronicler of his active life, was equally desirous to aid in the furtherance of knowledge of man and his antecedents. Together they participated in and made possible the field studies which serve in part as a foundation for this book.

PREFACE

This book is based in large part on field work and firsthand dissections; it stresses function more than is usual in textbooks of comparative anatomy. It leans heavily, as do all present-day anatomical texts, upon the great contributions of the past. Many of the facts it presents have been painstakingly gathered, particularly in the past two centuries, by careful workers in Germany, England, Italy, and France, and to an increasing degree in the Western Hemisphere. Such great investigators as Malpighi, von Baer, Goethe, Gegenbaur, Wiedersheim, Owen, Darwin, Huxley, Lamarck, Cuvier, Mivart, Pasteur, Cope, Osborn, and Gregory, to mention but a few of the contributors to the discipline, have unearthed facts and built generalizations upon them. These ultimately affected and determined the philosophic viewpoint of the present age to the extent that evolution, change or mutation, and dynamics dominate the present philosophy of man.

The expression "Faustian outlook" or "Faustian soul" is heard frequently today. In essence the expression refers to ceaseless striving, the enthronement of intellectual curiosity, the daemonic but controlled urge to understand, harness, and really see natural phenomena. Combined with this quality is that of action, experiment, and interference with processes and structures. With this outlook the weight of the past may be undervalued, the innumerable steppingstones that led to the present may be underestimated. In this ruthless drive to penetrate the mysteries that surround life or the organization of matter and the nature of energy, the small voice of reflection may be stilled.

Meanwhile, as recipient of the life and energy spark in a unique measure, man has made it his duty and found it his compulsion to spend years in the laboratory instead of in the sun, to throw life after life into investigation and research, in order that someone, somewhere, may advance knowledge. This compulsion complex and its results reminds one of the secret the great plain below the pyramids and the nearby pyramids themselves hold. Over 100,000 nameless slaves are reputed to lie buried in this field, representing the cost in human blood of their achievement—the towering monuments in their midst. This segment of the past had its planners, its architects, its mathematicians, its masons, its laborers, its water boys, and its whips working together to the end that

great monuments might grow. The picture is symbolic of the present striving of the Faustian soul.

The author is indebted to his publishers for many courtesies received during the preparation of this manuscript; to Margaret Holman, Joseph Lucas, John Schubart, and Virginia Willard for the drawings; to Armour and Company, Parke Davis and Company, Sharp and Dohme, the General Biological Supply House, Ward's Establishment, the American Cyanamid Company, the J. B. Lippincott Company, Whittlesey House, the Macmillan Company, *The Scientific American*, Elmo Perkins of the Lincoln Zoo, Chicago, Dr. Detlev Bronk and Dr. Edward Dunkle of the Cleveland Museum of Natural History, and Dr. John Warfel, for the use of certain drawings and photographs; to Thomas Lannon, head of the Art Department of the Cleveland Clinic, for the photography of many of the illustrations; to Dr. A. H. Hersh of the Biology Department of Western Reserve University for critical reading of the manuscript; and to his wife Marion Quiring for the preparation of the manuscript. The many thankless tasks incident to preparing the copy, correcting the manuscript, and checking data fell to her.

Finally, a great debt is acknowledged to Dr. J. S. Kingsley, comparative anatomist, who instilled an abiding interest in the subject during the author's apprenticeship with that master.

DANIEL P. QUIRING

CLEVELAND, OHIO
July, 1950

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INTRODUCTION

LEVELS OF BEING

This work is an attempt to portray comparative vertebrate anatomy from a viewpoint somewhat different from that generally presented in textbooks of this nature. For a number of years, with the late Dr. George Crile, the author has had the privilege of observing and dissecting in their natural habitats many of the creatures whose parts are briefly described in these chapters. In observing living vertebrate animals, one is impressed by the fact that in their performance or behavior they obey the principles of their architecture. The alligator does not attempt to move from his niche. He is held to it more rigidly than is a member of the most exclusive Indian caste. His lot is determined by the sum total of his anatomy. He is the slave of the sun and apparently never rebels against the chains by which he is bound. These are the chains of limited sensory development, of cold-bloodedness, of a vestigial cerebrum, of a limited lung capacity, and small heart and blood volume. When we compare his performance with that of an impala buck in his prime, we are introduced into a new world of protoplasm, for the impala is so highly organized that from the standpoint of the machine, of the physics of motion, he would appear to have no rival on land. Yet when we look into the sky and follow the man-of-war bird in flight, we are witness to another world into which protoplasm has ventured several times, in different guises. Bird and bat conquerors are at perfect ease in this milieu. Bone, muscle, heart, eye, brain, and wing are so adapted to flight that a level of being is achieved that is a source of constant wonder when we explore and consider the mechanisms that have brought it about.

Where does man stand in the light of these achievements of impala, bat, and bird? At first glance he does not fare too well from a physical viewpoint. The impala outruns and outsmells him. Until recently the bird outsoared him. The bat has a radar system built into his sensory apparatus which apparently has no counterpart in man. Yet we may not dismiss man lightly, even in the physical sense. Physical dexterity is evident when he plays the piano, paints a picture, or guides a pen in writing a clear sentence. In song the regulation of his vocal chords

equals and perhaps surpasses the action of the syrinx of thrush or mockingbird. His greatest achievements, however, are along other lines. In brain and psychic development he has outdistanced all rivals. This places him on the highest living achievement level, and while this may be but the bottom rung of an evolution of spirit or of functions which we see dimly today, it appears to be of the essence of that which lies at the heart of organic development.

It is from this viewpoint that the author has ventured to introduce into these chapters the concept of levels of being. This viewpoint in no way implies a static creation with fixed or predetermined boundaries. Mutation is the magic wand which transforms one level into another. Constant struggle keeps the species strong and receptive to change, unless it happens into the pitfall of excessive specialization.

Whether or not the student accepts the underlying philosophy is immaterial. The idea of levels of being is not new. Lamarck, and long before him Aristotle, recognized the concept in the sense of a fixed creation of types moving within fixed boundaries. As used here, it does not have these connotations—it implies simply the stage of development of bodily systems reached by a group, as expressed in performance and behavior.

CHAPTER 1

FORM AND STRUCTURE

THE SHAPE OF THINGS

The forms or shapes of animal bodies fall into definite patterns. These patterns represent the visible expression of physical and chemical laws. We have no difficulty in visualizing the manner in which a particular mountain or hill or valley is formed. Upthrusts of the earth's crust produced a mass jutting high above the surrounding level. Storm, wind, cold, heat, rain, ice leave their mark. If the high mass is of soft earth, it soon crumbles. If it is granite, the weathering is slower. In time, its form or shape reflects the forces which work upon it. A drop of water or other fluid takes characteristic shape because of the forces, in this case surface and internal tension, which act upon the fluid.

When we consider animal form, the problem becomes more involved, since we are dealing with a labile substance which grows and modifies itself and seems at times to contradict or counteract the inanimate forces which act in the universe. However, when we analyze animal form or shape, we find that it cannot escape such forces as gravity, surface tension, cohesion, temperature, to mention but a few of the agents which act upon it.

The sphere is one of the fundamental forms which many invertebrate bodies assume (Fig. 1). Spherical shape gives certain advantages; the relative surface for a given mass is large in the small and small in the large sphere. If it is desirable to conserve heat, this shape becomes an important factor in larger bodies. Small bits of protoplasm expose a relatively large surface given such a form. Amongst chordates, however, the true sphere is rarely approached, although many subordinate body organs do assume this shape, *e.g.*, brain, kidneys, liver, and heart. A modification of the sphere, the cylinder, is more common. This retains some of the advantages of the sphere in conserving surface area and adds a new one, since the elongate cylinder is better adapted, given the proper skeletal foundation, to engage in rapid movement. Land animals generally have adopted this pattern. The body of an alligator, horse, cow, man resolves itself into a series of cylinders of varying sizes.

Arms, legs and digits are cylinders, and this design is built deeply into the architecture of the land animal.

Another shape is the spindle. This is in keeping with good streamlining and is the almost universal pattern of fishes, in which it represents an adaptation to water life. Bird form, while a modification of the

spindle, actually is more akin to the pattern of the falling drop. Analysis shows it to be a combination of cylinder, sphere, and spindle.

These then are the general patterns of animal form. Organisms breed true to them, since these designs are built into their genetic architecture and persist for long generations, unless some force disturbs the genetic design, when modifications may follow. The biologist assumes, for example, that the fish was ancestral to the land animal. If this is true, it means that in time the spindle shape of the fish became changed to the cylindrical form of land inhabitants.

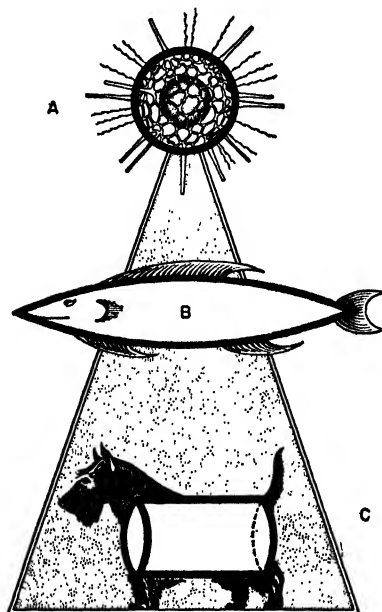


FIG. 1. Basic body shapes. A, the sphere is common in invertebrates; B, the spindle in invertebrates and chordates; C, the cylinder, the usual shape of land vertebrates.

STRUCTURAL ADAPTATIONS

It becomes apparent when one surveys the vast world of vertebrate animals that form and structure are not the fixed, immovable entities they seem upon superficial examination. Our

viewpoint is often limited to the survey of a living animal or group which happens to be existing contemporaneously with us. If we delve into the past history of the present forms and trace their ancestry in so far as we can from the bony fossilized fragments which have been unearthed, we see them as labile stuff upon which the environment, as a combination of all the forces operating from without and within, has been working. Just as in the case of the mountain, heat and cold, sunshine and rain, gravity, and other forces have been shaping

and adapting animals to certain conditions. The term *adaptation* takes on an almost mystical significance in biology. It is used to denote the unconscious structural responses of animals to a changing environment, their ability to make new responses to a given environment, or the mere condition of fitness, regardless of any change. Those groups generally which failed to respond with new or changed structures when the external environment was altered are no longer here, while those which did are of a tough fiber, able to meet a variety of conditions. Their progeny has seeded the earth.

Structure is another convenient biological term to indicate the particular architectural specifications of an animal. Form represents the outer appearance—the shape which it assumes, determined by the underlying structure. When we consider structure, we naturally turn to the *skeleton*, although the term applies to any of the bodily systems. Skeletal structure shows clearly the effect of the myriad forces by which animals have become adapted to various habitats. The fish skeleton, a rather simple affair if the backbone alone is considered, shows little differentiation throughout its length. It reflects the habitat in which the fish lives. Body muscles are attached along the entire column; their primary function is to propel the animal. With the appearance of land life, entirely new demands were imposed upon the animal body. It was lifted from the ground; it was physically supported; muscle and skeletal elements were transformed into lever systems; and in this evolution the entire body became adaptively changed. Some of the amphibians, not divorced from aquatic life, retained a relatively unchanged skeletal system. In frogs and toads, on the other hand, skeletal specialization occurred to such an extent that locomotion proceeds in a series of jumps, a new type of vertebrate movement, although widely employed and of ancient lineage among the saltatorial invertebrates.

Other skeletal specializations appeared in those mammals among which running became a common mode of progression. The skeleton not only carries the weight of the standing animal but is so correlated with its muscular attachments that great speed may be developed. One small group of mammals, perhaps forced to the trees by more aggressive neighbors, developed the habit of brachiating. This means of locomotion, whereby the animal uses its forelimbs in swinging from branch to branch or from tree to tree, had the further effect of freeing the forelimb from the primary task of supporting the body weight, as happens in the four-footers. This increasing freedom of the forelimb was one of the factors which finally placed one insignificant genus of the primate order in a position of power and dominance out of all keeping with its relatively

meager body strength. Man's ancestry, over a period of some 40 million years, was the repeated beneficiary of adaptive mutations which resulted in his becoming, at least in his own estimate, the chosen species that has lorded it over lesser animal creation.

Perhaps the most subtle and delicate of all skeletal and dermal adaptations occurred in the land ancestors of the birds. Derived from a reptilian stock, they not only developed wings and pneumatic bones but exchanged scales for a new type of skin derivative, the feather, and to make this unbelievable mechanism more wonderful and efficient, as constant high temperature was included in the specifications.

MUTATIONS

What is the mechanism of change whereby skeletal or other body part, are transformed? The answer to this question evaded earlier workers although many developed interesting speculations concerning it. Gregor Mendel, the Austrian monk, found the key which enabled later investigators to open the door to this secret. It had been known since the days of antiquity that animals breed true to type. Mendel, by his patient plant-breeding experiments, found that characteristics appear as unit characters and that these factors are carried over to new generations in definite mathematical proportions.

In 1900 Hugo De Vries, responsible for the term *mutation* as it is used in biology today, described his observations on the evening primrose (*Oenothera lamarckiana*). He noted that the type and size of plant, leaf, and flower were apparently determined by the number of chromosomes in the germ cells. He termed the variants he observed in this genus mutations. Subsequently it was shown by Muller, Thomas Hunt Morgan, and other workers that minute changes in the chromosomes, produced by chance or by man's willful manipulation, may call forth new characteristics in the animals whose cells have been so interfered with. Since the chromosomes are the carriers of the hereditary characteristics, it is obvious that changes in these carriers might alter the nature of their possessors.

This key in the hands of the experimenters developed into more than a theory of evolution: it became the mechanism of evolution. Its correctness is attested by the fact that the experimental geneticist may actually transform one species into another in the laboratory. This key, which the biologist calls mutation, is his explanation for the vast host of plants and of both invertebrate and vertebrate animals which have arisen presumably from a common ancestral stock.

This idea of evolutionary method by accumulation of mutations,

while called Neo-Darwinism, is quite different from the Darwinian theory. Although Darwin held that one species might be transformed into another through the accumulation of small variations, he did not recognize the controlling factor. He believed that minute changes appearing in an isolated species would in the course of time produce new groups sufficiently far removed from the old to warrant their designation as new species. Today it is known that, unless heritable changes occur in the chromosomes of an animal, it will breed indefinitely according to the pattern of its ancestry. We are tied to our past unless chance or willful interference produces changes in the determiners of our inheritance. Thus chromosomes determine our level of being, and only through changes in them may that level be changed.

LEVELS OF BEING

Living animals, because of the chromosomal mechanism for inheritance and change, occupy definite levels of being; they live on specific plateaus determined by their degree of development. Each animal group has become distinctive because of a number of characteristics peculiar to itself. The sum of such attributes adapts the animal to a certain mode of life, and this mode of life determines the animal's position with reference to its environment. These conditions seem fixed, for, as indicated, animals breed true for generations, reaching the same level, never overstepping the boundaries set by their chromosomal determiners. We may go back 25,000 years in man's history without finding any marked changes in his physical development. From this standpoint he appears static. True, he has not yet exhausted the possibilities built into his nervous machinery, but this has not altered his level of being. It is a unique plateau on which he dwells, not approached by any competitors, although in the matter of food getting and reproduction he does not differ basically from other vertebrates. It is in his mental activities by which he tries to explain himself and the universe about him that he reaches a level far above that of any other animal. The combination of his peculiar body build and his mental equipment, determined by his chromosomes, has fixed his position.

The qualities of the ape fit him for a particular environment; he occupies a definite niche in nature, or rather he has, unconsciously, hewn out a definite niche for himself because of his peculiar attributes. These fix his level of being. A survey of the animal kingdom indicates that many such specific plateaus exist and that they are determined by the specific characteristics of the animals occupying them.

In a sense the scientific classification table is a graphic picture of this

concept, for in this scheme animals are arranged in order of increasing complexity and relationships. The highest categories in the classification represent the highest levels of existence.

It has been emphasized that the degree of development of the systems of the body determines the level of being. This may be shown graphically. Thus Fig. 2 shows the degree of brain development in certain vertebrates. Brain weights have been plotted against body weights.

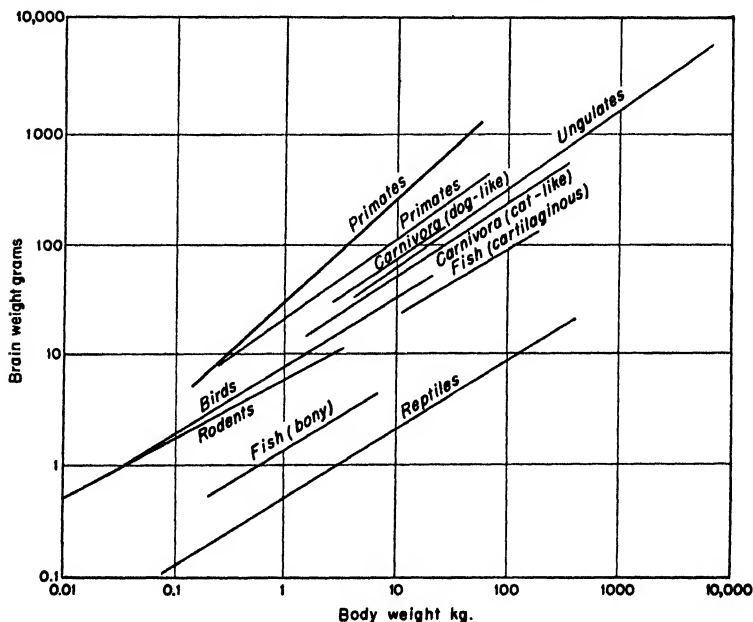


FIG. 2. Graphic representation of the different cephalic levels of various vertebrates.

Reptiles occupy one position on this graph, indicated by the line running through the plotted points marking reptilian brain weights. Rodents, in comparison, take a higher position, ungulates another, while the primates reach the highest level. Within a given class of animals the increase of brain weight proceeds quite regularly with increasing body weight, but if a 50-kg. fish is compared with a 50-kg. carnivore or with a 50-kg. primate, the difference in position on the graph becomes obvious. Similar graphs may be constructed for other systems, and it may be

shown that the animals experiencing the greatest development of organs controlling energy release occupy the highest positions on such a life scale.

This is revealed further when the organs controlling energy release are compared in such widely divergent animals as the lion and the alligator, for example (Fig. 3). Table 1 indicates the weight of these systems in the two animals. The skeletal and muscular weights of one

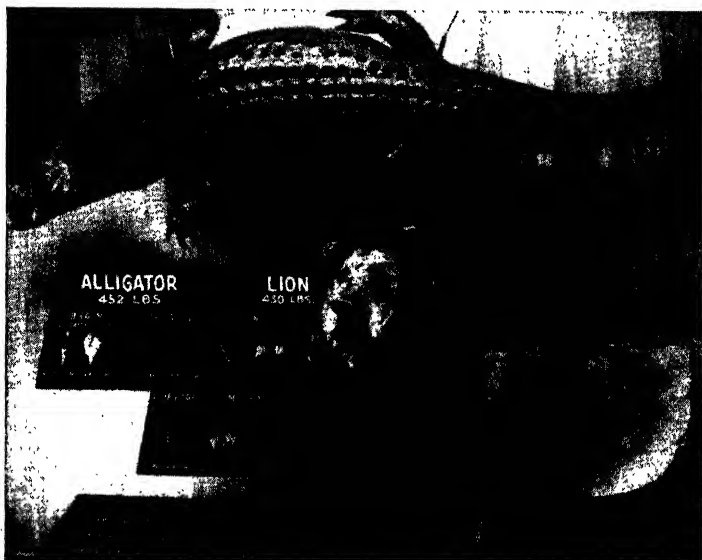


FIG. 3. Alligator and lion differ greatly in behavior and energy expenditure, presumably because of differences in development of certain key systems.

animal about equal those of the other. When brains, adrenals, thyroids, hearts, livers, and lungs are compared, however, great differences emerge. These differences, we must assume, are responsible for the difference in performance of the two animals. The cold-blooded condition itself in the alligator appears correlated with an extremely small brain, just as a certain minimum of brain size is associated with the warm-blooded condition. In the light of the functions of these key organs, a comparison of their weights shows clearly that the alligator cannot spend energy at the rate of the lion, for its glandular constitution causes it to occupy an entirely different plateau of performance. Actual basal metabolic

studies show that a 53-kg. alligator produces approximately 53 cal. of heat in 24 hours at 22.1°C. The warm-blooded lion in this example, if he produces heat at the rate of a man, will release 5740 cal. in 24 hours.

TABLE 1. COMPARISON OF WEIGHTS IN ALLIGATOR AND LION

Animal	Body wt., kg.	Brain wt., gm.	Adre- nal wt., gm.	Thy- roid wt., gm.	Heart wt., gm.	Liver wt., gm.	Lung wt., gm.
Alligator.....	205	14.08	11.36	13.32	318	522	628
Lion.....	191	261.00	34.64	22.52	1,175	5,725	2,300

Taken by itself, the concept of levels of being presents a static picture of the animal world, but it is only part of the story, since it sets off and dissociates animal groups from each other. The idea of relationships is not inherent in the idea of levels. Yet animal groups are related to each other. They were not created in piecemeal fashion. The chemical elements hold within themselves the power to combine in various ways to produce organic growth. The unbelievable world of plants and animals about us is an expression of the power within these chemical elements. Time permitted the appearance of more varied and more complex living forms. The earlier ones gave rise to the later; all stand in definite and specific relationships with each other. These family connections resulted in a definite hierarchical order among animals comparable to (but more complex than) the ladder-like position in which child, parent, and grandparent stand with respect to each other. Each generation was in a unique relationship to the rest. It is much easier to see the levels reached by animal groups than to observe the relationships that tie them to each other. The idea of relationship introduces the dynamic element in biology; it implies growth, development, change. It indicates the continuous operation of the great forces that mold, maintain, and reproduce the species but at the same time offer the species constant opportunity for change. The principle of ever-changing flux is inherent in these relationships. The flow of living substance, cutting new channels into the inorganic universe and abandoning or completely transforming old ones, thus presents a dynamic continuity that has persisted and grown from the very beginnings of organized life.

The concept of levels of being has other biological implications. Within a species, for example, we recognize different levels. By proper selection we may breed and segregate various characters. In the human

race apparently chance selection has produced plateaus within the group. No one will deny that great musical or mathematical gifts run in certain families, or that certain individuals are endowed with a restless physical energy, or that others are moody, inert, and sluggish in behavior. More and more we attribute many such peculiarities to differences in the physicoglandular constitution of the individual. The time may not be far distant when it will be recognized that even our political viewpoints are colored by our thyroid-pituitary-gonadal secretions or by the amount of sunlight available to our bodies. Part of the destructive effects of ghetto and slum are due to the absence of sunlight, lack of physical exercise or work, and the consequent effects on psychic behavior. The sociologist and social worker might very well advance their field study greatly by a thorough foundation in the biological sciences. Many of the superficial suggestions for "reform" would, under realistic treatment, take different shape.

THE CELL

We have seen that structure determines the position of the animal in the life scale. When we analyze structure in the living body, we find that it depends upon microscopic components, the cells. The cell is the structural unit of protoplasm, and as such it forms a logical foundation for any biological study. In animals, cells are organized into tissues, organs, and organ systems, and it is the province of the comparative anatomist to study these cell combinations.

Today the cell is looked upon as a dynamic entity. It is an organic unit made up of combinations of chemical elements (Fig. 4). These elements are present as carbohydrates, fats, and proteins; they appear as electrolytic solutions, crystals, colloids, formed bodies, and cell inclusions. Their organization in the cell is highly specific, and the latter owes its specialized functions to this exact structure. The activity of the cell is regulated largely by two of its parts, the nucleus and the cell membrane (Fig. 5). Everything that enters or leaves the cell does so through the semipermeable surface membrane, whose behavior is regulated by the principles of osmosis, diffusion, and permeability. The nucleus, in addition to its function as regulator of immediate cellular activities, carries in the specialized germ cells the determiners, or hereditary characteristics, called genes, arranged in linear order in the chromosomes. Membrane, nucleus, and other cell constituents are present in an electrically disturbed or unbalanced state. Like a flame, they are constantly changing, yet the pattern remains ever the same. The degree of restlessness of this changing state may be measured in terms of

oxidation, excretion, variation in electrical charge, growth rate, changes in permeability, and so forth. It is significant that, so long as the cell shows life properties, it carries electrical surface and nuclear charges as well as charges on the colloidal and crystal particles and the formed bodies within.

This conception of the dynamic nature of the cell has been well described by Ludwig von Bertalanffy; the following paragraph is based largely on his description.

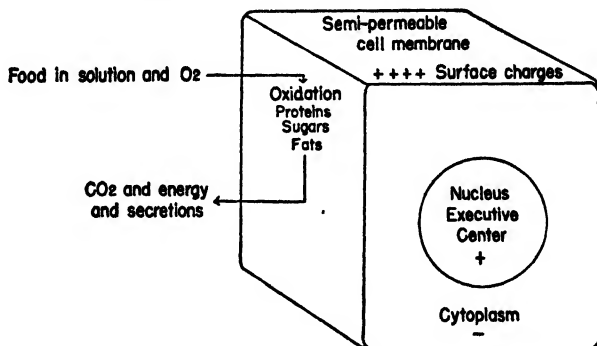


FIG. 4. The cell is a dynamic entity in which various reactions bring about release of mechanical, chemical, and electrical energy. It forms the structural foundation for tissues, organs, and organ systems. The nucleus, or executive center, contains chromosomes which in the germ cells are the carriers of hereditary characteristics.

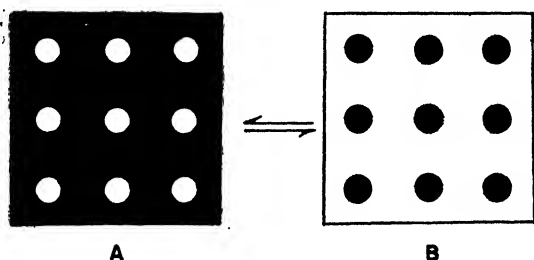


FIG. 5. The cell membrane is a labile structure. The black area in A represents the fat, or lipoidal, substance of the membrane in the continuous phase when fat-soluble substances pass through the membrane. In B, the lipoidal substance is in the discontinuous phase, and the water, represented by the white area, is in the continuous phase. Under these conditions, water-soluble substances pass through the membrane, and fat-soluble substances are held back. The shift from phase to phase is probably determined by changes in the electrical charges of the cell membrane.

According to modern atomic physics, all forces active in material bodies are those surrounding electrical particles in a magnetic field (Fig. 6A, B). Living organisms, too, represent electromagnetic systems, and vital processes must finally be of electrical origin. Since the

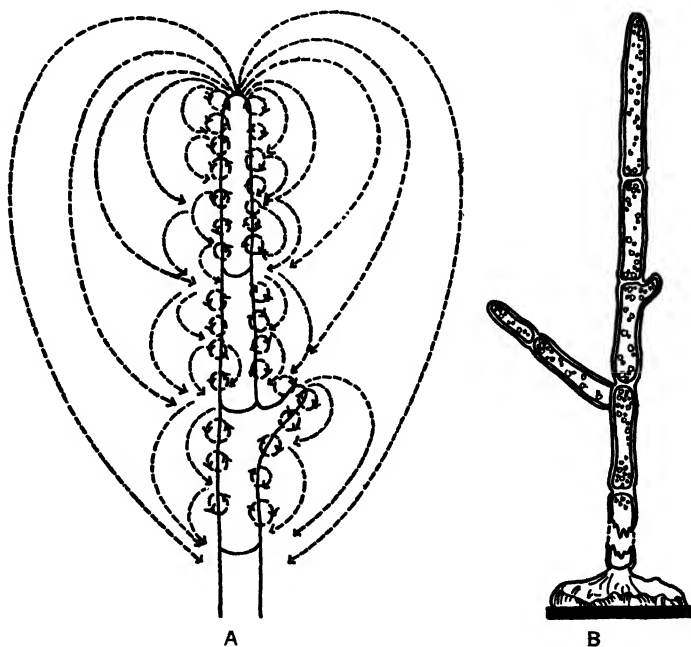


FIG. 6A. A schematic portrayal of the electrical potential differences between various points in three cells, including an apical cell of *Pithophora*. Greatest difference is encountered between the apical and third cell. Smaller differences may be demonstrated when closer intervals are compared. (After Lund.)

FIG. 6B. Cells and apical buds of the plant *Pithophora*. Electrical potentials of varying intensities are associated with the activities of these cells, as with all cells. The greatest potential difference is encountered between the apical cell and the older cells. These potential differences presumably reflect the metabolic and growth activities of the plant. (After Lund.)

organism represents a differentiated and dispersed system, the intensity of the electrical field may change rapidly from point to point. The size of various particles within cells is of the order of 10^{-6} , and the potential difference between adjacent particles is roughly 10^{-1} . The strength of the electromagnetic field may be 100,000 volts per sq. cm. in such a system. Such colossal field strengths exhibit great energy mani-

festations in the organisms. Actually the functions of respiratory, vascular, and other organs are correlated with specific potentials, as shown by selective staining. The tubuli of the kidney, for example, are strongly charged negatively; they absorb water and sodium chloride by electroosmosis, and they therefore excrete positively charged urea. One concludes that electrical phenomena are causal for the functioning of the organism.

As self-maintaining bioelectrical systems the cells serve as collectors and spenders of energy. In carrying out their vital processes they utilize energy, and in this use they obey the first and second principles of energy conservation: they transform some of it into useful work, heat, and radiant and electrical energy, while the remainder may be stored as potential energy or dissipated. Their ultimate energy source is the sun. The plant by its synthesis of carbohydrates through the interaction of sunlight, chlorophyll, and water and by its building up of fats and proteins makes energy available to the animal cell. The object, then, of all nourishment is the capture of energy, either for immediate or for future use.

THE APPROACH TO THE ANIMAL

The evolution of animals includes development of complex energy-releasing systems and energy-collecting systems by transformation of the single cell state. The animal is a composite of organ systems working together to a common end, which is its continued existence and its reproduction (Fig. 7). This it does through utilization of energy. The orderly working together of these parts is controlled by nervous system, ductless glands, and chemical agents produced in the body generally (Fig. 8).

The study of the animal body may be approached by various methods. *Embryology* deals with the appearance of tissues, organs, and systems in the individual, *histology* with their microscopic structure, *physiology* with their function. *Ecology*, a study of animal communities and animal habitat, reveals the living animal in relation to its environment, while *chorology* considers the factors that control animal distribution. *Genetics* represents a search for the factors that control inheritance. *Comparative chordate anatomy* concerns itself with the appearance, development, evolution, and comparison of the structures of animals that have in common a supporting column. This column may be a single supporting rod, called the notochord, or a series of articulating cartilages or bones, the vertebral column.

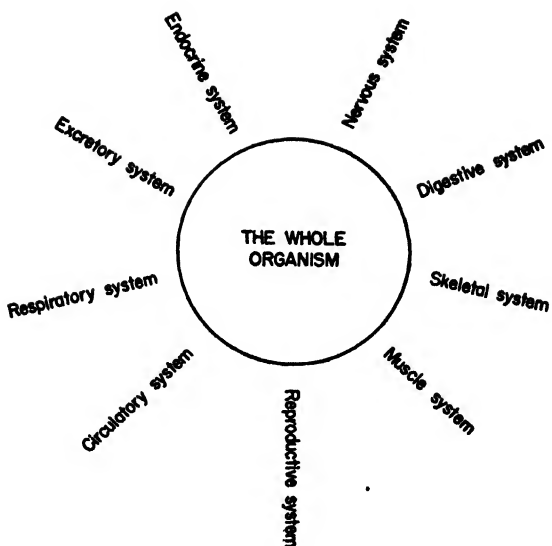


FIG. 7. The systems of the organism. Collectively, these systems are the organism. Their orderly working together is a necessary prerequisite to life on a high metazoan level.



FIG. 8. Two male chicks of the same breed and age; the bird on the right has been injected with a male hormone extract (androsterone). Note the difference in comb and wattle growth in comparison with the control bird on the left.

SIDELIGHT

Taken by themselves, the concepts "form" and "structure" have little meaning. Considered in the light of function, they are a key to the understanding of the particular animal under investigation. In our work in the field with a great assemblage of animals, intermingling in their feeding or fighting for the possession of favored areas, the meaning of form and structure became more obvious. Apparently no animal disputes with the elephant. One morning while on the trail of a small elephant herd we came to a halt near a rhino pool. In the dim forest ahead two large elephants were suddenly discerned at rest in the deep shade. At a distance of 50 yd. we tested the wind in the hope that

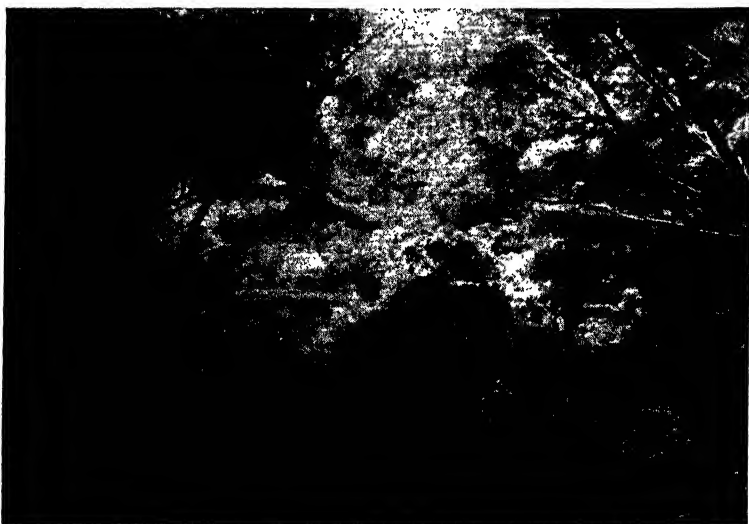


FIG. 9. Elephant country. The forest in cooperation with the sun builds up and stores energy; the elephant in its shade utilizes it.

an advance within good camera range might be possible. While we were waiting, a pair of rhinos, whose eyesight is as poor as that of the elephant, came to a halt about 40 yd. to the right of the elephants, each pair unaware of the other. With a momentary change of air currents the rhinos scented the elephants, and off they crashed without any hesitation, leaving no doubt in our minds as to the influence of structure in this particular case. Apparently lesser animals willingly give way to the elephant. The structural adaptations of animals to particular functions are innumerable. A chimpanzee on the alert follows a different action pattern from that adopted by the zebra; the zebra dashes away without hesitation; the chimpanzee may follow these tactics but soon returns to a

favorite feeding ground. On his return he climbs occasional high trees at the forest edge and carefully surveys the area. His climbing ability has enabled him to utilize this method of spying out danger. Behavior is determined by structure.

A realistic approach is necessary to gain even a partial understanding of form and structure. The animal conforms to the principle of cause and effect. Given an organ or system of a certain type, this will be utilized; in its absence the habits and habitat are accordingly modified. At times an association of animals appears to follow Dalton's law of gases. In a mixture of gases, each gas behaves as far as pressure is concerned as though it alone were present. At other times animals show attractions and repulsions as though they were so many electrical charges of like or unlike kind. These reactions represent responses to structure.

Prolonged studies of individuals or of associations of animals has led the author to the conclusion that energy release is perhaps the key to an understanding of comparative anatomy and physiology. It appears to be the central feature written into the specifications of form and structure. The architecture of bone and muscle, of eye and brain has been well explored; the key role of energy-controlling systems, however, is only now coming under intensive critical scrutiny (Fig. 9).

SUMMARY

We have seen that animals have definite form and shape, that their structures represent adaptations to specific types of environment. The mechanism for producing change is mutation, which is possible because of the nature of the chromosomes, the carriers of hereditary qualities.

Adaptive changes lead to various levels of being. Ultimately we find in the cell the unit upon which the entire labile and dynamic animal mechanism is based. The cell is the medium through which energy may be utilized. Cell combinations and organizations form animals, and these animals spend energy in varying amounts.

Man represents the highest level of achievement of protoplasm. He exists for a brief interval at a given level. At best he represents an unstable combination of elements, a highly improbable state, as Boltzmann, the Austrian physicist, indicated years ago. Once reaching a high level of organization, he starts on the pathway to disintegration, to a more probable condition that does not make the impossible and incessant demand for continuous adjustment, self-repair, and self-building. The ultimate stage of nirvana is reached when the particles, originally filled with fire, with ruthless ambition or with high thought and striving, sink to a state of heat death, the most probable state, where heat no longer flows and complete entropy is reached. For a few moments the organic combinations transcend their chemistry, as does the cortical

nerve cell when it creates a Beethoven Ninth Symphony or a Shakespearean sonnet. These are temporary achievements of the organism. All too soon energy degradation appears, and the magic protoplasm becomes dust.

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CHAPTER 2

CLASSIFICATION

PURPOSE

The purpose of biologic classification is to group in systematic order the diverse plant and animal types that have appeared on the earth. A natural system of classification attempts to arrange plants and animals according to relationships. Classification is valuable, not only in fixing the position of the animal in the natural scheme, but also in suggesting underlying trends of the evolutionary process. If we accept the theory of special creation, according to which each species was formed by a specific act of the Creator, classification has meaning only as a formal catalogue of events. On the other hand, if we accept the theory of evolution and assign animals to groups according to the natural order of their appearance and development, classification becomes a key to their relationships. Thus it offers an up-to-the-minute inventory of living as well as of fossil animals and the key to the hierarchic relationships of animal groups as they appeared under the guidance of time.

While time does not enter as a definite factor into classification, the idea of time is inherent in any scheme that portrays the unfolding and evolution of living things. With the development of his science, the biologist acquires increasing respect for time. He assumes that it is real and irreversible and that animals appeared on the earth in definite temporal sequence. Great geologic periods have passed, each with characteristic land and water surfaces, each with its own peculiar climates that determined the nature of the flora and fauna of the respective periods (Table 2). Many plants and animals of former times have persisted, some unchanged, while others by mutation have given rise to new forms. Many did not persist, and their fossilized structures help to bridge the gap between the organic world of today and that of the remote past. In a sense, classification summarizes what natural forces have accomplished with 93 natural elements under the dominance of time (Fig. 10).

In the animal kingdom, living stuff has congealed or condensed into nearly a million species, of which approximately a twentieth, or 50,000, belong to the chordate phylum. The major stopping points in the

sequence of animal forms have been established as follows (Figs. 11, 12, 13):

PHYLUM CHORDATA

Subphylum Protochordata

Class Hemichordata

Class Urochordata

Class Cephalochordata

Subphylum Vertebrata

Class Cyclostomata

Class Pisces

Class Amphibia

Class Reptilia

Class Aves

Class Mammalia

THE AGES OF LIFE ON EARTH

Eras	Ages	Periods	Approximate duration	
CENOZOIC	(Quaternary) Age of Mammals	Recent		
		Pleistocene First men—Glacial period	1 million years	
	(Tertiary) Age of Mammals	Pliocene Elephant—Rhino—Deer	6 million years	54 million years
		Miocene Mastodon	12 million years	
		Oligocene Paleotherium—(Seasons appear)	16 million years	
		Eocene Placental mammals—Primates	20 million years	
MESOZOIC	(Secondary) Age of Reptiles	Cretaceous Flowering plants—Apogee of Dinosaurs—Ostriches—First snakes—Many insects	40 million years	135 million years
		Jurassic Swimming and flying dinosaurs—First reptile like birds—Archaeopteryx—(No seasons)	60 million years	
		Triassic Reptiles, dinosaurs, tortoises, crocodiles—First mammals (Marsupials)	35 million years	
PALEOZOIC	Age of Amphibians	Permian First ammonitidae (Mollusks)—Sphenodon	25 million years	360 million years
		Carboniferous Batrachians (Stegocephala)—Selachii—Ferns, cordates—First reptiles	85 million years	
PROTEROZOIC	Age of Fishes	Devonian Fish—Ostracodermi—First ferns—Insects—First batrachians (?)	50 million years	360 million years
	(Primary) Age of Invertebrates	Silurian First ganoid fish—Marine plants—Mollusks—Cephalopodes	130 million years	
		Cambrian Crustaceans—Trilobites—Polype	70 million years	
ARCHAEOZOIC	(Algonian)	Traces of worms (Annelida), Crustaceans—Trilobites (Arthropodes)	Estimated duration (After W.A. Parks, F.R.S.C.: About 800 million years, or 2/3 of the age of life on Earth, and 1/2 of the age of the Earth itself)	1200 million years
	(Archean)	Bacteria (Microscopic organisms—Leptothrix)		
		Pre-Cambrian		
		Traces of life in the form of local deposits of coal.		
			All figures in this column are approximate but based on the most authoritative modern works.	

TABLE 1a.

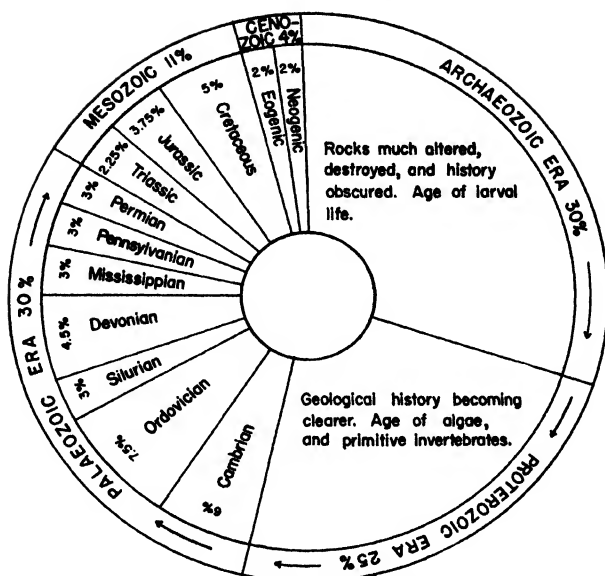


TABLE 1b. (Redrawn from Schubert.)

Outer Space
Sun, Planets
Other Stars
Galaxies

Atmosphere

Living Plants and Animals

Earth Crust
(93 elements)

FIG. 10. Organic evolution depends upon the 93 elements as building stuff. These elements act upon one another under the influence of an atmosphere and within a temperature range prevailing upon earth to the end that organisms with specific properties are formed. Sun, gravity, and other influences act upon and mold these organic entities.

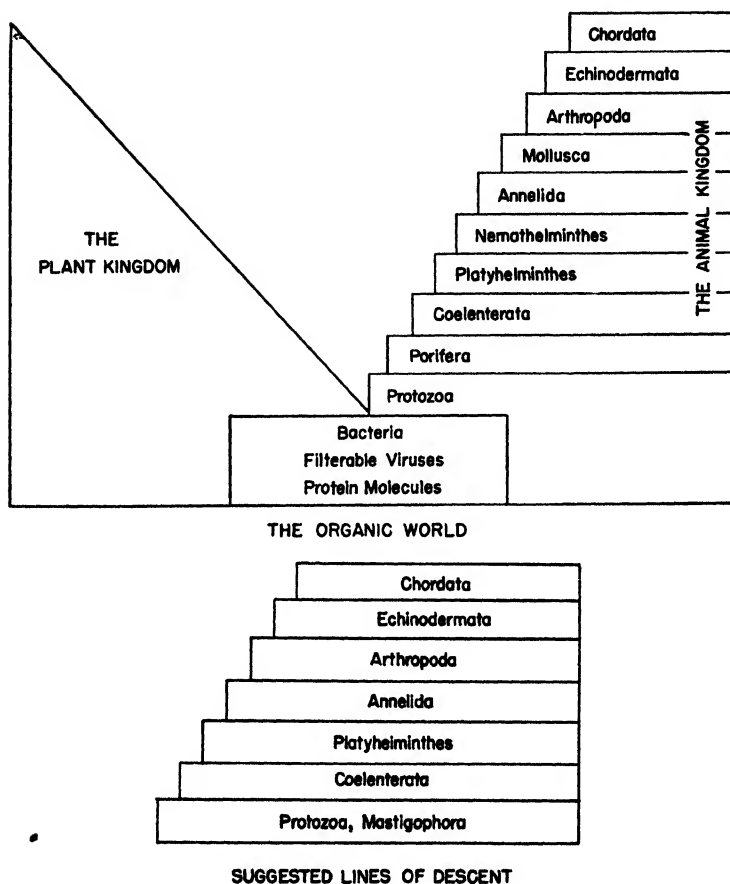
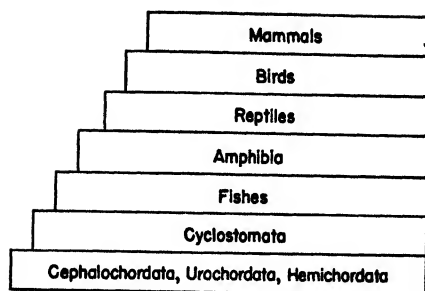
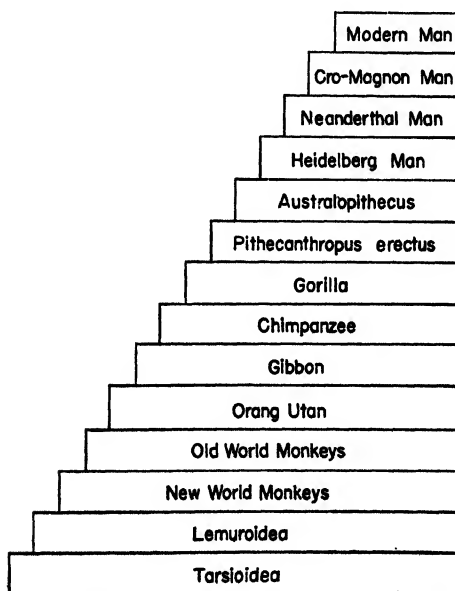


FIG. 11. Suggested line of descent of the chordate phylum. Presumably the chordate ancestry has passed through some of the indicated stages before the phylum reached its present status.



CHORDATE PLATEAUS

FIG. 12. The chordates have separated into well-marked aggregations designated as classes, each with its own body of common characteristics which distinguish them from the remainder.



THE PRIMATE STOCK

FIG. 13. Within the class Mammalia, one order, the Primate, has become differentiated into a number of distinct families, some extinct. At the head of these various families one genus, Homo, has assumed a position of leadership. This genus consists of a single living species.

The binomial system, introduced by Linnaeus (1758), is employed in naming animals. According to this system, both genus and species names are used to designate a given animal scientifically, as in *Homo sapiens*. However, to orient an animal completely, we begin with a much broader term than genus or species, the designations becoming increasingly restrictive until the individual is reached. For example, the following categories are used to classify a horse:

Kingdom Animalia
Phylum Chordata
Class Mammalia
Order Ungulata
Family Equidae
Genus *Equus*
Species *caballus*
Individual horse

As we have noted, the chordate phylum is divided into two subphyla, the protochords, or Acrania, with three classes, and the vertebrates, or Craniata, with six classes. The first two classes of Protochordata, the Hemichordata and Urochordata, have few qualifications for membership in the Chordata if their adult phase alone is considered; but they are included in the phylum because in embryonic development a notochord, a dorsal nerve, gill slits, and a pharyngeal gill chamber are present. The third class, the Cephalochordata, retains typical chordate features throughout life.

Class Hemichordata

The hemichords are worm-like animals that live buried in the sand at tide levels. Their embryology is suggestive of the echinoderm phylum, in that the larva, known as the tornaria, has the ciliated appearance of the pluteus stage of the sea urchins. An acorn-like proboscis marks the anterior end, while posterior to this is a membranous collar under cover of which a mouth leads into the pharynx. Gill slits permit water to circulate between the pharynx and the outside. The notochord appears as a slight diverticulum dorsal to the digestive tube. As in the higher chordates, a dorsal nerve cord develops from the ectodermal plate, but here the similarity ceases, since hemichords have no brain, segmental nerves, or specialized sense organs. *Balanoglossus* is typical of the group (Fig. 14).

Class Urochordata

The urochords appear to be either degenerate or primitive chordates. In their larval stage they are free-swimming tadpoles with definite tail, segmental musculature, dorsal ganglion, and notochord (Fig. 15).

After a short larval life the body organs are transformed, and the tail is absorbed, except in the orders Appendicularia and Thaliacea. In the adult phase the remaining urochords, the Ascidae, are small, sessile, sac-like organisms; the vital parts are entirely covered by a tunic at-

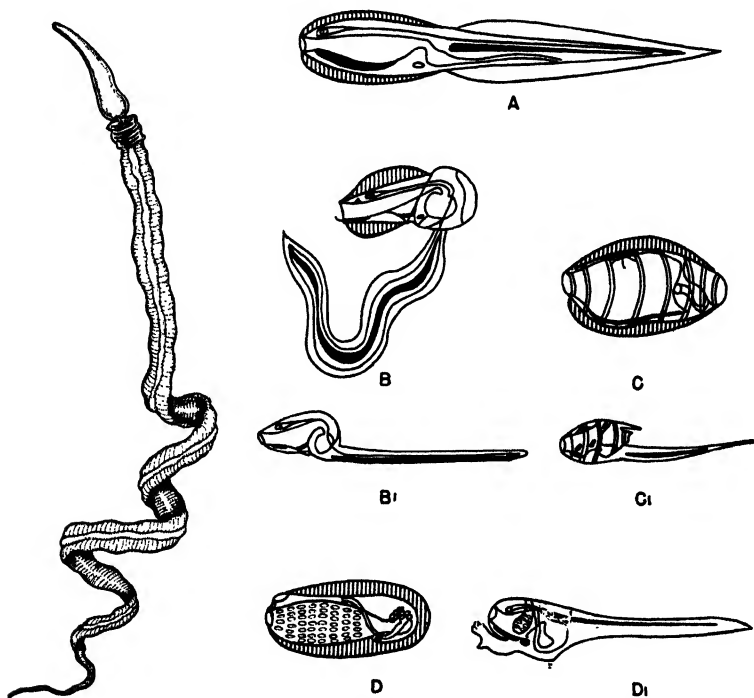


FIG. 14

FIG. 15

FIG. 14. *Balanoglossus* is a representative of the class Hemichordata.

FIG. 15. Diagrams of various tunicates. A, original tunicate type. B and B1, Appendicularia; B, sexual generation; B1, larva. C and C1, Thaliacea; C, adult; C1, larva. D and D1, Ascidia; D, adult; D1, larva. (After Kükenthal.)

tached at one end to the substratum. At the upper end of the sac an incurrent and an excurrent pore permit ingress and egress of sea water, which circulates freely through the pharynx. Removal of the tunic reveals the pharynx, perforated by numerous gill slits and surrounded by an atrial chamber. The digestive tract originates on the pharyngeal floor and continues as a coiled tube to the anal opening near the atrial pore. A groove extends along the floor of the pharynx, comparable

with the endostyle in the pharyngeal floor of *Amphioxus*. It is believed that the epithelial lining of this groove is the precursor of the thyroid gland in higher vertebrates. The notochord disappears in the adult, while the dorsal nerve cord, reduced to a small ganglion, is placed between the incurrent and the excurrent pore under cover of the tunic. The urochords are hermaphroditic. A single gonad lies near the curvature of the digestive tube.

General structural variations occur. Only the Appendicularia retain a tail in the adult stage. It is bent about 90 degrees to the left of the long axis of the body, and the intestine does not extend into it. The Thaliacea lose their tails but retain their swimming habits and move by contractions of the body wall, which is surrounded by isolated bands of circular muscles. The Ascidaceae, or sea squirts, become completely sessile, attaching themselves to the substratum in colonies in which some division of labor is apparent.

The urochords, considered primitive rather than degenerate by some investigators, because in some species celom and segmentation are lacking, exhibit also a reversible heartbeat, asexual reproduction, and colonial habits. The ancestral tunicate was probably a free-swimming, tailed, tadpole-like animal with a distinct division between the anterior portion, which was covered by the tunic, and the caudal portion, provided with a notochord and ciliated digestive tract. Figure 15, based on Lohman's drawing, shows the changes that mark the phylogeny and the individual history of these animals.

Class Cephalochordata

The cephalochords are small, fish-like animals ranging from 1 to 3 in. in length (Fig. 16). Living in coastal waters, they inhabit the tropical and subtropical seas of the world. *Amphioxus*, better named *Branchiostoma*, a member of this class, was first described in 1774 by Pallas, who based his account on a single preserved specimen. He classified the animal as a sea snail. Since then it has been variously designated as a new order of fish, an annelid, or a cyclostome.

In outward appearance *Amphioxus* is lance-shaped. A continuous membranous dorsal fin and two lateral membranous metapleural folds extend along the sides of the body. A short caudal fin gives the tail an arrow-shaped appearance. The anterior end indicates clearly that the animal is not a fish. The mouth in particular differs from that of fishes in the absence of a lower jaw, since it is a cone-shaped oral hood with a fringe of cirri around the base. The typical "herringbone" arrangement of the segmental body muscles is revealed through the

semitransparent body wall and is common to cephalochords, cyclostomes, and fishes. These segmental muscles promote rapid and efficient lateral movements and are the chief locomotor organ. Median fins and lateral folds apparently serve as rudders. Specialized abdominal, branchial, and anal muscles have also developed in connection with these organs.

The mouth leads into the pharynx, which is supported by interrupted cartilaginous rods. Between the rods openings permit water to enter the atrial chamber. The latter surrounds the pharynx and opens at the midventral atrial pore, slightly anterior to the anal aperture. The pharynx leads directly into the straight digestive tract lined with cilia. The pharynx has a grooved floor, the endostyle, and an epibranchial

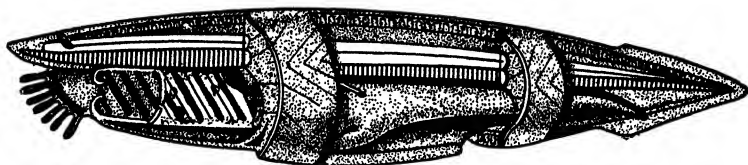


FIG. 16. *Amphioxus* (*Branchiostoma*). A small, spindle-shaped marine cephalochord. (After Parker and Haswell.)

groove in its middorsal line. Caudally the intestine terminates at the anus. About midway in the tract a ventral liver diverticulum grows anteriorly, remaining permanently attached to the intestine.

The circulatory system forms a complete circuit from heart to arteries, capillaries, veins, and back to the primitive heart. The latter consists of a sinus venosus and chamber. A ventral vessel, the truncus arteriosus, below the pharynx, sends blood to the gills for aeration; from there it passes to the dorsal aorta just above the gills, and thence it is distributed to the organs of the body. From the intestine the blood is sent through a capillary network, the hepatic portal system, to the liver and is returned to the heart. The general pattern of this circulatory system resembles that of fishes, although the heart is so primitive that it is more akin to a pulsating tube than to a true heart.

The nervous system is distinguished by a dorsal nerve cord surrounded by a sheath of connective tissue continuous with the notochord. The brain with a ventricle or hollow space in its center is a slight ganglionic thickening beyond the anterior end of the notochord. Segmental nerves emerge from the cord, as in vertebrates, but dorsal and ventral nerve roots are not united, and cranial nerves are not specialized. An auto-

onomic nervous system, represented by isolated sympathetic fibers, passes to the viscera.

The sexes are separate. Secondary sexual organs are not developed, and paired gonads are permanently retained within the atrial cavity.

We observe in *Amphioxus* characteristics suggestive of later and more highly specialized animal forms. Notochord, closed circulatory system, hepatic portal system, pharyngeal breathing apparatus, segmental musculature, and segmental nerves represent its primary qualifications for inclusion within the chordate phylum.

VERTEBRATA

A higher level of being than that of the protochords is obvious in the vertebrate subphylum; in the latter six well-defined classes already indicated are recognized. Each class undergoes its own peculiar bodily and organic development, separating it from the others, and within each class differences arise, correlated with variations in the size of respective systems. Thus in birds we recognize grain-eating, insectivorous, and carnivorous species, and correlated with these habits striking external and internal structural changes have appeared within the class. Further, the Aves are separated from other classes by distinctive features.

Class Cyclostomata

Cyclostomes, comprising the lampreys and hagfishes, are the most primitive of the vertebrates (Fig. 17). They fall naturally into two subclasses, each represented by a single order, the subclass *Hyperoartii* represented by the order *Petromyzonoidea* and the *Hyperotreti* by the *Myxinoidea*. Because they have a true brain case, as do the remaining vertebrates, they are called *Craniata*, in contrast to the three protochordate groups, designated as *Acrania* because a skull is absent. In *Amphioxus* the anterior end of the notochord supports the base of the simple brain, but in the cyclostomes supporting parachordal and trabecular plates appear, together with cartilaginous capsules surrounding the inner ear. In outward appearance the cyclostomes, cylindrical and tapered at both ends, resemble the eels, which are true fish. The respiratory system of 5 to 15 gill openings in each side of the body leads to internal gills. While lower jaw and paired fins are lacking, dorsal and caudal fins occur, supported by cartilaginous rays. The skin is naked, with an ectodermal layer copiously supplied with mucus-secreting cells. On the inner surface of the jawless, cone-shaped suctorial mouth are horny teeth, varying in number with the species. Eyes are present although vestigial in some myxinoids. A single nasal opening on the

dorsal surface of the head leads into a cul-de-sac. The thyroid gland is foreshadowed by an endostyle of specialized cells, which line a groove in the floor of the pharynx. The heart has a single ventricle, an atrium, and a sinus venosus. A ventral aorta leads from the ventricle to the afferent branchial arteries. The latter terminate in a capillary bed in the gill, confluent with the capillaries of the efferent branchial arteries. These arteries unite into a dorsal aorta through which the blood is distributed to the body. The circulatory channels form a continuous closed system, characteristic of the vertebrates. The embryo passes through blastula and gastrula stages, ending with the hatching, when the young may or may not resemble the adult animals.

The myxinooids, or hagfish, entirely marine in distribution, undergo direct development without a larval stage. The eyes are degenerate and may be covered with skin. A spiral valve is absent in the intestine, and

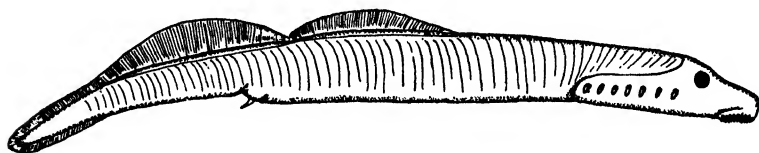


FIG. 17. Lamprey is a typical cyclostome; its larva is known as ammocoetes.

the pronephros persists throughout life. Only seven pairs of cranial nerves are developed. The integument is provided with numerous mucous glands. When the animal is restricted, these glands may secrete large amounts of mucus, converting the surrounding water into a viscous mass. This characteristic accounts for the species name, *glutinosa*, given to the genus *Myxine* by Linnaeus.

The petromyzonoids, or lampreys, occur in both fresh and salt water. In contrast to the myxinooids they undergo metamorphosis, passing through a characteristic larval stage known as *ammocoetes*, which may persist for 3 years or longer. At metamorphosis the lens, retina, and corneal layer of the eyes undergo marked development, and the eyes are supported by optic capsules. Changes in the mouth transform it into a suctorial organ. Seven gill openings lie on each side of the pharynx. Ten pairs of cranial and one pair of spinal occipital nerves occur. In the adult a functional pronephros is retained, and the sexual organs become functional.

The myxinooids follow a peculiar method of external parasitism. First attaching itself to the body wall of the host, the animal either eats its way into the body cavity or enters the gill openings. Some of the myxi-

noids, after gaining entrance to the pharynx of a living fish, fill the mouth cavity of the victim with mucus and, when gill movements cease, penetrate into the abdominal cavity, devouring liver, heart, intestine, and muscle.

Class Pisces

Fish were among the first vertebrate animals to be studied systematically. Aristotle (384–322 B.C.) recognized and classified several hundred species. Earlier than Aristotle the Egyptians demonstrated knowledge of Nile and Mediterranean fish in their paintings. Haeckel, the German biologist, for example, was able to identify 11 species pictured in a single Egyptian tomb. In recent years, particularly with the acceptance of the evolutionary theory, both living and fossil representatives have been studied intensively with reference to their ancestry and their possible connections with land animals (Fig. 18).

Fish fall naturally into two great divisions, the Chondrichthyes, with a cartilaginous skeleton, and the Osteichthyes, with a bony one.

Subclass Chondrichthyes

Order Cladoselachii: extinct sharks

Order Elasmobranchii (elasmobranchs): dogfish and sharks

Order Rajiformes: rays and torpedoes

Order Holocephali: Chimaera

Subclass Osteichthyes

Order Dipnoi: lungfish

Order Crossopterygii: Osteolepis

Order Actinopterygii: all remaining living fish

Suborder Chondrostei: sturgeon

Suborder Holostei: gar pike

Suborder Teleostei: codfish, salmon, etc.

Chondrichthyes. *Elasmobranchii* and *Rajiformes*. The most primitive of living fish are the elasmobranchs of the suborder Selachii (Fig. 19). Most elasmobranchs are marine, although living as well as fossil fresh-water representatives have been found. The skeleton is cartilaginous, a feature common to all Chondrichthyes. On each side five to seven gill slits open directly to the outside without a protecting operculum, or gill covering, such as is found in bony fish. Embedded in the skin are placoid scales which show closely similar structure to the teeth of land vertebrates. The spiracle on the dorsum of the head connects the pharynx with the outside. A spiral valve offering a wide surface for food absorption is a distinguishing feature of the intestine. Paired pectoral and pelvic, single dorsal, caudal, and abdominal fins occur. In the male the pelvic fins are extended into claspers. Fins



FIG. 18A. *Dunichthys terrelli*, representative of the giant armored fishes which lived in an inland sea covering the eastern area of what is now the United States, some 350 million years ago. The late Peter A. Bungart, paleontologist and expert in the preparation of fossil fish, is shown in the background. (Courtesy of the Cleveland Museum of Natural History.)



FIG. 18B. *Cladoselache*. A fossil imprint of a Devonian shark presumably ancestral to later cartilaginous fishes. (Courtesy of the Cleveland Museum of Natural History.)

are supported by cartilages. The tail is not symmetrical but sweeps upward with a larger dorsal extension and a smaller ventral one. Such a tail is *heterocercal*. Many elasmobranchs give birth to live young and are therefore ovoviviparous, in contrast to egg-laying, or oviparous, bony fish. Actually the eggs are retained in the oviduct during development without appearance of a true placenta, although a yolk-sac placenta occurs in some sharks. This type of viviparity is an instance of delayed egg laying. Most elasmobranchs are aggressive and carnivorous in food habit.

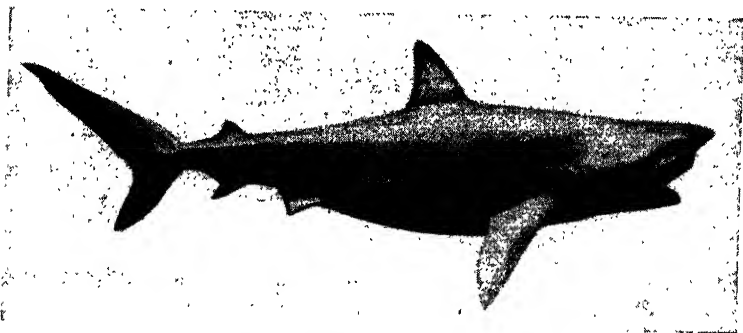


FIG. 19. The tiger shark, a typical elasmobranch.

Included in the class are dogfish, shark, skate, ray, and torpedo, the latter capable of inflicting severe electric shocks through segmental muscles transformed into electric storage batteries. In the rays, the body has undergone a remarkable transformation in that the pectoral fins are transformed into great lateral wings by which the fish moves. As a result, the greatly flattened rays are adapted to life on the ocean floor or to shallow coastal waters.

Holocephali. The Holocephali, a small marine order, combine certain characteristics of cartilaginous with those of bony fish. Claspers are retained as in the elasmobranchs but a spiracle is absent. The upper jaw is firmly united with the skull (holostylic) as in the Osteichthyes. The grotesque fish *Chimaera* is the outstanding representative of this class (Fig. 20).

Osteichthyes. The remaining fish, grouped under the subclass Osteichthyes, constitute about 90 per cent of all fresh and salt-water species. With the exception of the Chondrostei and Holostei, they are distinguished, as the name indicates, by a bony skeleton. Externally they are characterized by paired pectoral and pelvic fins, a homocercal

tail with equal dorsal and ventral dermal extensions, a bony operculum covering the gills, and an air bladder. The latter is a balancing organ in some species and an auxiliary breathing organ in others. Most species have scales which according to their appearance are named

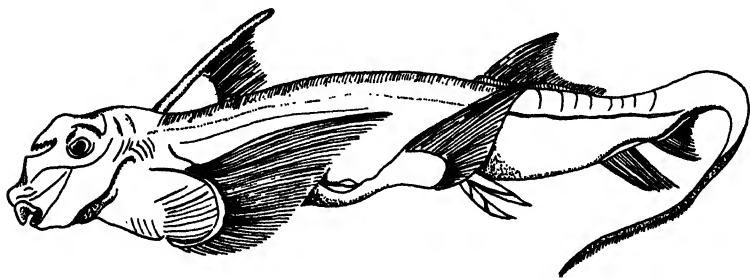


FIG. 20. The Chimaera, or rattail, is a holocephalian fish with large head and smooth skin. The mouth is provided with grinding plates. (After Parker and Haswell.)

cycloid (circular), *rhomboid* (shaped like a parallelogram), *ctenoid* (having toothed projections), and *ganoid* (having an enameled ganoid surface over a bony scale). Some bony fish are without scales.

Dipnoi. The Dipnoi, in some respects the most remarkable of living fish, are capable of two modes of breathing, thereby assuring their self-maintenance in a changing environment (Fig. 21). When the streams

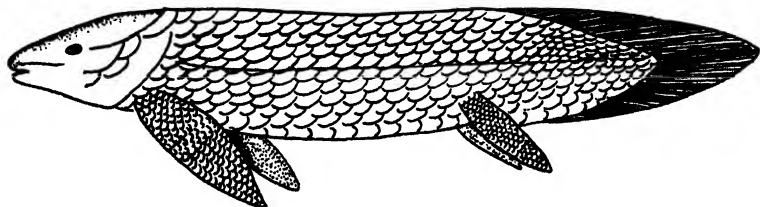


FIG. 21. *Neoceratodus*, the Australian lungfish, has narial channels extending from the nasal sacs to the roof of the mouth.

which they inhabit become dry, these lungfish estivate, buried in the mud of the stream bed. As the mud coating dries, they adapt themselves to air breathing through the swim bladder, which acts as a lung. With the advent of the rainy season the mud case gradually dissolves, and they again breathe with gills. This behavior suggests how the transition from gill-breathing to lung-breathing animals may have oc-

curred. Dipnoi are limited to a fresh-water habitat; the genus *Protopterus* is found in Africa, *Lepidosiren* in South America, and *Neoceratodus* in Australia.

Crossopterygii. The *Crossopterygii* are lobe-finned fish (Fig. 22A, B.) Believed extinct until 1938, a living specimen (*Latimeria chalumnae*)

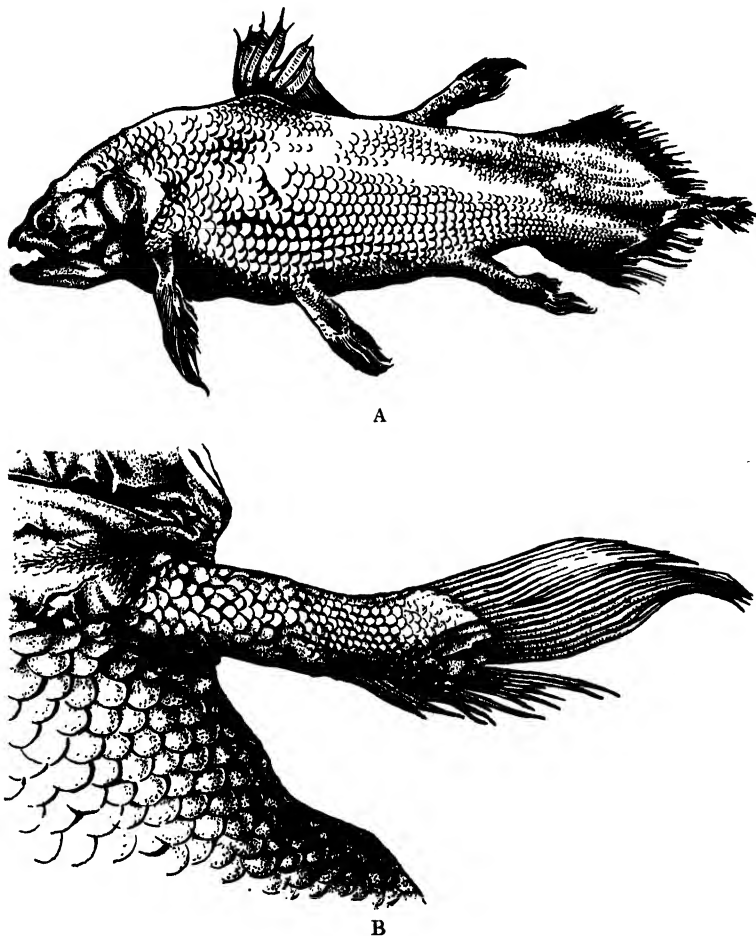


FIG. 22. A, *Latimeria*, presumably the only living crossopterygian fish. This suborder was believed extinct until a specimen was taken off the South African coast in 1938. B, detail of pectoral fin and body scales. (Redrawn from Smith.)

was taken in that year off the coast of South Africa. Unfortunately its condition was such that little was learned of its internal anatomy. These lobe-finned fishes are closely related to lungfish and are considered possible ancestors to land animals. A characteristic external feature, the basal lobe of the pectoral fin, supports and perhaps propels them along the ocean floor. The margins of the fins are fringed, and their bases are covered with scales. Other features are a spiracle, paired dorsal fins, and a *diphycercal* tail into which the spinal column extends in a straight line, dividing the caudal fin into equal dorsal and ventral halves. Spiral valves are retained in the intestine, and the swim bladder is transformed into a lung.

Actinopterygii. The spiny-finned fish constitute the order Actinopterygii, which contains three sub orders.

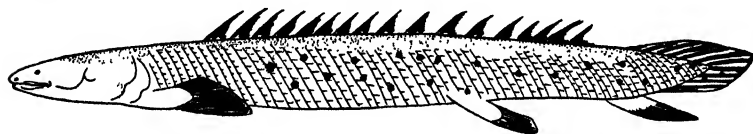


FIG. 23. *Polypterus* is a typical chondrosteian fish with ganoid scales and skeleton predominantly cartilaginous. (After Messer.)

The sub order Chondrostei includes *Polypterus*, the ray-finned fish; *Polyodon*, the spoonbill; *Acipenser*, the sturgeon. The skeleton is largely cartilaginous, the skin is covered with rhomboid or cycloid scales, and a primitive heterocercal tail is retained along with a spiracle (Fig. 23).

The sub order Holostei includes gar pike and bowfin. The skeleton is largely bone, scales are of the ganoid type, the tail is *homocercal*, and a functional respiratory air bladder and spiral valve are present. Generally the dorsal fin is short and lies far caudad; the pectoral and pelvic fins are widely separated. Both Chondrostei and Holostei are ancient types marking the transition between cartilaginous and bony fish.

The sub order Teleostei includes the remaining spiny-finned fish which constitute the vast majority of fresh- and salt-water species (Fig. 24). They dominate all others in number and excel them in range of distribution, pattern, and specialization. They are adapted to such varied habitats as the surface or the profound depths of ocean, to arctic waters or hot springs. They include winged forms, finless writhing eels, and abbreviated giant sunfish. Body weights range from less than an ounce to several hundred pounds. In many species the swim bladder is closed; in others, although the swim bladder is alveolar and has an

opening into the esophagus, it apparently does not possess respiratory functions.

Land and air had been conquered long before the arrival of the vertebrates. Aquatic invertebrates, presumably through mutations, gave rise to both land and air inhabitants, each with its characteristic mode of locomotion, one through the development of appendages capable of supporting and conveying the body on land, the other through the magic of wings. From what source did the push come, and in which group did the yeast of change first produce the structure and biological courage to venture on land? The indirect evidence points to the crossopterygians. Their lobed fins, capable of lifting and moving the body along the ocean

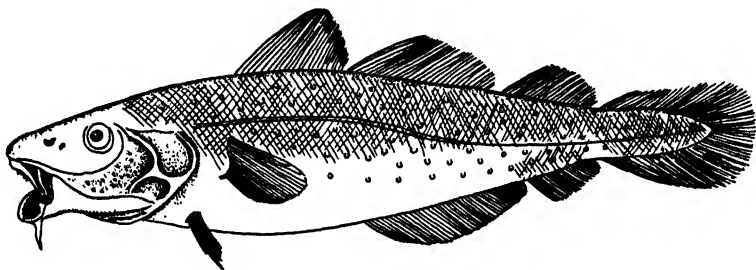


FIG. 24. The cod is a typical marine bony (teleost) fish. (After Parker and Haswell.)

floor, and their alveolar swim bladder apparently conferred advantages that were probably not neglected by adaptive mutations. These changes appeared in causal sequence, and great time cycles were required for the unutterably slow alterations.

Apparently modifications first centered in the paired fins and in the swim bladder. Pectoral and pelvic fins and heavily muscled tail, although ideally adapted for balance and locomotion in the water, could not furnish sufficient support on land. In the new body patterns no systems remained unchanged, but all evolved in such relation to each other that increasing energy utilization for the demands of the new habitat became possible. Modifications included gradual transformation of the swim bladder and gill arches, rerouting of the circulatory channels, subdivision of the heart chambers, and specialization of the musculature. The backbone, forming the central arch of the skeletal structure, was redesigned with a series of strengthening supports and new articulations at points of strain. Pelvis and pectus were gradually transformed into lever mechanisms that not only supported increasing

body weight but made possible agility and swiftness of movement. Increasing awareness was another demand of the new habitat upon the organism. The brain in fish, primarily an olfactory organ, increased its integrating function in land animals and became more responsive to visual and auditory impressions. Ductless glands, regulating a wide variety of adaptive responses to both internal and external stimuli, increased in relative size and function and bettered the chances for self-maintenance and reproduction.

Class Amphibia

Amphibia, true to their name, lead a double life. All begin as aquatic animals; some forsake this medium with the acquisition of lungs, others by retaining gills are restricted to water, still others lose gills and fail to develop lungs—in these the skin takes over the respiratory function. Amphibians first appeared some 400 million years ago in the Upper Devonian period. They represent the first successful vertebrate invaders of the land. Their chief characteristics are cold blood, skin usually naked although sometimes provided with bony scales, and a heart with a single ventricle and two atrial chambers. Lungs, gills, or skin serves as breathing organs. The following orders constitute the class Amphibia:

Order Stegocephalia (*e.g.*, *Trematops milleri*): extinct amphibians probably derived from crossopterygian fish

Order Gymnophiona (*e.g.*, blindworm): naked amphibians without limbs, resembling worms

Order Caudata (*e.g.*, *Necturus*): naked, tailed amphibians, some breathing with gills, others through the skin

Order Salientia (*e.g.*, frog): naked, tailless lung breathers with a skeleton specialized for hopping.

Stegocephalia. The Stegocephalia, extinct precursors of Amphibia, once were represented on both land and water. Forming a connecting link between crossopterygian fish and true amphibians, they were probably ancestral to reptiles as well, since they resemble closely an extinct reptilian order, the Cotylosauria. Elongate animals with well-developed tails, heavy skull armor in some cases extending over the abdomen, labyrinthodont teeth, and double occipital condyles, they had an extremely small brain case and an elongate lower jaw with fewer bones than those of bony fish (Fig. 25). The skull resembled that of living amphibians and reptiles. Vestiges of a lateral line system persisted. Notably in skull and limb development they show advances over living

amphibians, since with the exception of tailed and apodal orders the latter class is highly specialized.

Gymnophiona. Gymnophiona are limbless, worm-like amphibians confined to the tropics. Many of the 50 species are aquatic, although they may be nocturnal land feeders. Pectoral and pelvic girdles are

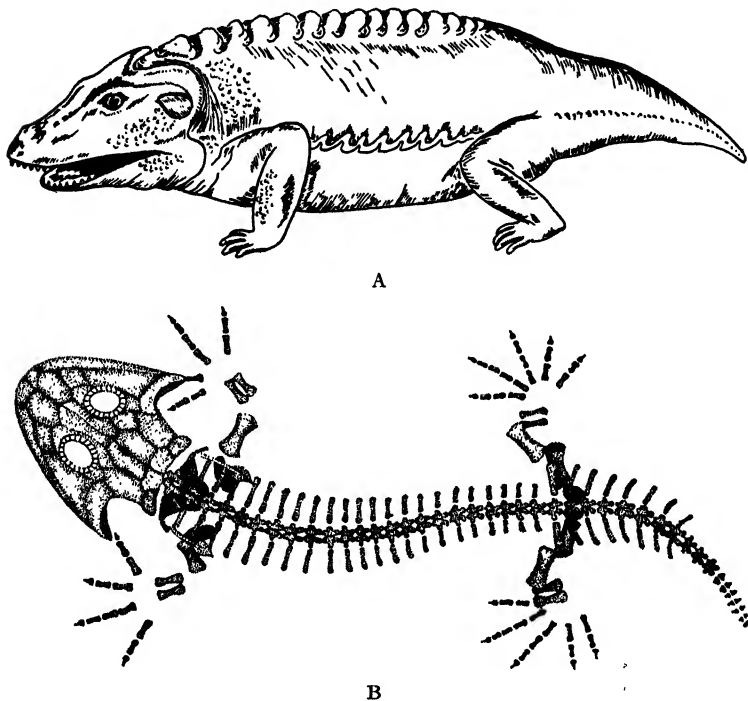


FIG. 25. Stegocephalia. A, artist's conception of *Cacops*. (After Fenton.) B, a skeletal reconstruction from the permian limestone formation near Dresden. (After Bronn.)

absent; the skin appears naked, although it has buried vestigial scales. A functional right lung and a notochord occur. The eye is degenerate. A small palp, probably sensory, lies between eye and nostril.

Caudata. Newts and salamanders, representatives of the Caudata, are, aside from frogs and toads, the best known amphibians (Fig. 26A). They may be aquatic or terrestrial, and if terrestrial they are restricted to damp areas (*e.g.*, salamanders). Three degrees of adapta-

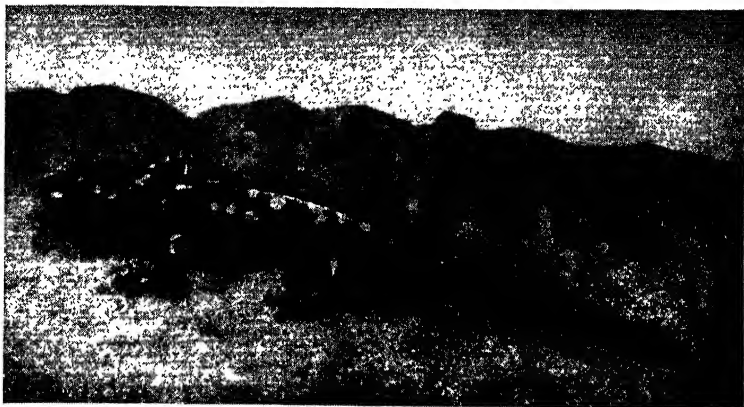


FIG. 26A. The spotted salamander *Ambystoma tigrinum* is an inhabitant of damp, mossy woodland areas. (Courtesy General Biological Supply House, Chicago, Ill.)



FIG. 26B. The frog, an anuran amphibian which after a tadpole stage loses gill and tail and breathes with lungs. (Courtesy Ward's Natural Science Establishment, Inc., Rochester, N. Y.)

tion to land life appear. The first is represented by the Perennibranchiata, characteristically aquatic and retaining gills throughout life, *e.g.*, *Necturus*, and *Proteus*, the blind European amphibian. The next stage is recognized in *Derotremata*, which remain aquatic although during metamorphosis elongate sac-like lungs replace all but one pair of gills and gill openings. The skin is naked and glandular. Typical of this group are the hellbender, or *Cryptobranchus* and *Amphiuma*. Newts and salamanders show a further adaptation to land life, with enclosed gills which may be replaced by lungs in some species; or failing to develop lungs they breathe through the skin. In the group as a whole primitive pectoral and pelvic girdles, permitting speedy locomotion, have appeared, and a well-developed tail is retained.

Salientia. The most highly specialized order of amphibians, *Salientia*, or *Anura*, is comprised of the toads and frogs (Fig. 26*B*). These animals pass through a tadpole stage in which they are aquatic, gill-breathing, and tailed. During metamorphosis these structures are replaced by lungs and highly specialized land limbs. Profound changes in skull, skeleton, and internal organization accompany these modifications.

Class Reptilia

Reptiles introduced a new protective device, the amnion, which converted them from free aquatic larvae by supplying the embryo with a liquid-filled sac, thereby decreasing the hazards of early development. All the previously described classes are known as *anamniotes*. Further, also in contrast to the *anamniotes*, reptiles never have functional gills. As a widely dispersed group of cold-blooded, lung-breathing animals, they inhabit water or land. The skin is dry and may be naked or covered with bony plates. The heart has two atria and a ventricle, the latter partly or completely divided into two chambers by an interventricular septum. A single occipital condyle provides articulation between the skull and vertebral column. During the great Mesozoic era, extending over some 90 million years, reptiles rose to a dominant position on land. The decline of the giant land dinosaurs must be attributed to failure of adaptation of the body to new conditions. Living reptiles are grouped in the following orders:

Order *Chelonia*: turtles, tortoises

Order *Rhynchocephalia*: lizards of the genus *Sphenodon*

Order *Squamata*: remaining lizards and snakes

Order *Crocodylia*: alligators, crocodiles, caymans

Classification. In addition to the four orders of living reptiles, a large number of extinct orders have been discovered. A complete

classification indicates the diversity attained by this group in the past. The following condensation of living and fossil orders is based on Storer's tabulation¹ which in turn is based on Romer's classification. Orders with living representatives are starred.

- ✓ Subclass I. Anapsida
 - Order 1, Cotylosauria: stem reptiles, Permian, Seymouria
 - Order 2*, Chelonina: turtles, Permian, Testudo
- ✓ Subclass II. Ichthyopterygia
 - Order 3, Ichthyosauria: Triassic, Ichthyosaurs, marine
- ✓ Subclass III. Synaptosauria
 - Order 4, Sauropterygia: Plesiosaurs, marine
- ✓ Subclass IV. Lepidosauria
 - Order 5, Eosuchia (ancient two-arched reptiles)
 - Order 6*, Rhynchocephalia: Triassic to recent, Sphenodon
 - Order 7*, Squamata
 - a. Lacertilia, lizards
 - b. Ophidia, snakes
- ✓ Subclass V. Archosauria (ruling reptiles)
 - Order 8, Thecodontia: Phytosaurus
 - Order 9*, Crocodilia: alligators, crocodiles, caymans
 - Order 10, Pterosauria (flying reptiles)
 - Order 11, Saurischia (reptile-like dinosaurs)
 - a. Theropoda (bipeds): Tyrannosaurus
 - b. Sauropoda (quadrupeds): Brontosaurus
 - Order 12, Ornithischia (bird-like reptiles)
 - a. Ornithopoda (bipeds): Camptosaurus
 - b. Stegosauria: Stegosaurus
 - c. Ankylosauria (armored dinosaurs)
 - d. Ceratopsia (horned dinosaurs): Triceratops
- ✓ Subclass VI. Synapsida (forms leading to mammals)
 - Order 13, Pelycosauria: Dimetrodon
 - Order 14, Therapsida (mammal-like reptiles): Cynognathus

As indicated, reptiles are further emancipated from a water habitat than are the amphibians, an emancipation that begins in the embryo with the appearance of the amnion and allantois. The amnion is a delicate encasement for the embryo, and the amniotic cavity, the space between this membrane and the embryo, is filled with amniotic fluid, offering a protected aquatic environment for the developing reptile. The allantois, a membranous organ supplied with a plexus of blood vessels, is closely associated with the inner surface of the egg, and through it the embryo gains oxygen and excretes gaseous wastes.

Other modifications have occurred in the adult reptile. Oxygen, no

¹ Tracy I. Storer, *General Zoology*, p. 632, McGraw-Hill Book Company, Inc., New York, 1943.

longer obtained from the water through gills, is breathed directly from the air into the lungs. This device greatly increases respiratory efficiency. The gill of a fish, for example, is exposed to 1 per cent of oxygen in water, whereas the lung of a turtle or of lung breathers generally is exposed to 20 per cent of oxygen in the air. Associated with lung breathing is a four-chambered heart with two atria and two partially complete or complete ventricles. Eggs, no longer laid and hatched in water, are variously developed and deposited on land. The eggs, retained in the oviducts of some snakes, permit the young to be born instead of hatched.

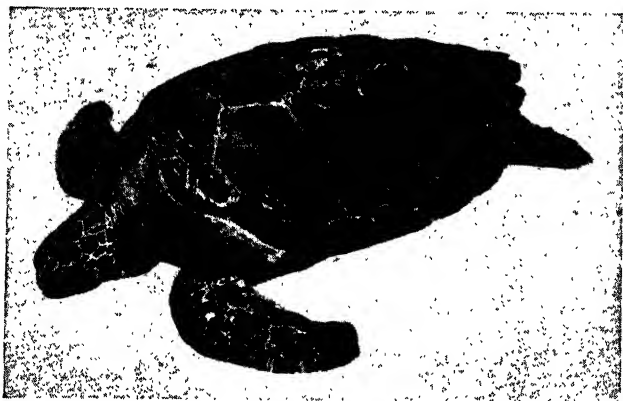


FIG. 27. *Chelonia*. The sea turtle is one of the larger representatives of present-day reptiles. This specimen weighed about 250 lb.; much heavier ones have been recorded.

Considerable specialization has appeared in reptiles, particularly among turtles and snakes. Turtles and lizards show great ability to use the limbs in lifting and transporting the body over the ground, while snakes have evolved a unique method of progression through adaptations of body muscles and ventral scales. New methods of defense—poison fang, sharp-edged cutting or crushing jaws, and constrictor muscles—have been factors in their survival. The brain is still classed as olfactory. Because of their cold-blooded state reptiles remain slaves to the sun; hence their distribution is limited by temperature.

The reptilian family tree begins with the *Cotylosauria*, an extinct group with affinities to the amphibian *Stegocephalia*, the latter in turn probably derived from the *crossopterygian* fish.

Living Orders. Among living reptiles the *Chelonia*, or turtles, are an ancient order in which the bony plates form a complete armor (Fig.

27). Internally they show a high degree of development of the circulatory system. The heart is relatively larger than that of the crocodilia, and the relative amount of blood is greater, indicating a higher level of performance.

The order Rhyncocephalia, represented by a single living genus, *Sphenodon* of New Zealand, is the only reptilian group found in that



FIG. 28. *Sphenodon*. This lizard, an inhabitant of New Zealand, is sometimes called a living fossil. It has a third eye in the dorsal surface of the head and retains other primitive skeletal features. (Photograph by F. N. Blanchard.)

country. It is a scaly, lizard-like animal reaching a length of 1 or 2 ft. (Fig. 28).

The Squamata comprise the lizards and snakes. The first division of this order, the Lacertilia, includes the chameleon and Old and New World lizards, of which only the Helodermata are poisonous. The second division, the Ophidia, includes all snakes, some 1,700 species, many of which are poisonous. The largest are the pythons, which may reach a length of 30 ft.

The Crocodilia include crocodiles, alligators, and caymans, all with powerful jaws, abdominal ribs, and heavily muscled bodies (Fig. 29). They are confined to tropical and subtropical regions.

Class Aves

Both birds and mammals trace their ancestry to the reptiles, the birds presumably evolved from the Archiosauria and the mammals from the Therapsida.



FIG. 29. Crocodilia. The alligator is characterized by dermal scales embedded in the skin and great muscular strength when the external temperature is sufficiently high.

Birds, judging from their numbers, are the most successful of vertebrate animals. Some 25,000 species and subspecies are recognized, compared with about 15,000 mammalian and a similar number of piscine. Outstanding is their power of flight, made possible by the evolution of feather, wing, pneumatic bone, modifications in breathing apparatus, and warm-bloodedness. Fossil remains of the earliest birds have been found in the Upper Jurassic in Germany. One of these, *Archaeopteryx*, a lizard-like, toothed bird, shows a close resemblance to the reptiles.

Classification

Subclass I. *Archaeornithes* (extinct toothed birds of Upper Jurassic)
Archaeopteryx

Subclass II. *Neornithes* (keeled or flat sternum, Cretaceous to recent)

Superorder 1, *Odontognathae* (extinct New World birds) *Hesperornis*, *Ichthyornis*

Superorder 2, *Palaeognathae*: *Ratitae* (walking birds) including ostriches, rheas, cassowaries, emus, moas, kiwis, *Aepyornis*, tinamous, with flat sternum

Superorder 3, *Neognathae*: *Carinatae* (modern birds, including some 23 orders with keel and ability to fly)



FIG. 30. The ostrich *Struthio* is the largest existing bird. Its brain is relatively small in comparison with that of the eagle. Its eyes are among the largest in the vertebrate assemblage. (Photograph from Anderson.)



FIG. 31. The tawny eagle, *Aquila rapax*, of Africa may congregate in flocks of 100 or more.

The ability to change their habitat at will accounts in part for the outstanding success of birds. Flight keeps them in touch with the maximum food supply and the optimum temperature. Moreover, flight permits them to breed in areas inaccessible to many enemies. Feathers provide the means for flight and for body insulation as well, enabling the bird to withstand greater rigors of climate than any other land creature, *e.g.*, the penguin of the Antarctic. The heart and specialized respiratory mechanism are greatly developed in all flying birds. Olfactory senses are no longer dominant as in the fishes. Instead, sight is extremely keen, especially in birds of prey; a visual acuity up to eight times that of man has been cited. The hard-shelled egg, built of lime salts, serves as a semipermeable membrane through which the embryo gains oxygen from the air and passes off carbon dioxide. In contrast to the reptilian embryo, incubation of the bird egg requires a high temperature (Figs. 30, 31).

Class Mammalia

Reptiles offer clues to the origin of mammals. The extinct Therapsida, which flourished in the Permian and Triassic periods, were mammal-like reptiles. Of this group, *Cynognathus* possessed a number of mammalian features. In contrast to living reptiles this genus had two occipital condyles; teeth were differentiated, and milk teeth were replaced by permanent teeth as in mammals. Pectoral and pelvic girdles firmly supported the body and enabled the long limbs to carry the animal freely over the ground. With these changes in the reptilian form came the differentiated backbone of specialized cervical, thoracic, sacral, and caudal elements. Hair replaced scales, and subcutaneous fat insulated the body from the external environment, aided in the retention of heat, and made possible the warm-blooded condition. The brain changed from an olfactory organ to a center in which the neopallium became the seat of delicate coordination and of memory.

Three great levels of organization represented by the following subclasses are recognized in the mammals: (1) Prototheria, (2) Metatheria, and (3) Eutheria. Within these subclasses other distinct levels, designated as orders, are apparent. Within the orders distinct levels of structure and performance are discernible.

Subclass Prototheria. Prototheria, or Monotremata, are primitive, egg-laying animals with incompletely developed mammary glands and without true nipples. The young are hatched from eggs and in *Echidna* attach themselves to the specialized hairs at the openings of the mammary glands in the marsupium of the mother. At the termination of

the nursing period this pouch disappears. The subclass comprises three genera confined to the Southeast Pacific area.

Ornithorhynchus, the Australian duckbill, is not easily recognized as a mammal, because it lives in an aquatic habitat, has webbed feet, possesses a bill instead of teeth except in the embryonic stage, and lays eggs. Heart, blood vessels, digestive tract, and brain are mammalian in type, although the corpus callosum which joins the two cerebral hemispheres in higher mammals is lacking (Fig. 32).

Echidna, the spiny anteater, and *Proechidna* are the two remaining genera. Their eggs are hatched as noted in a specialized skin fold, the



FIG. 32. Platypus, or duckbill, is semiaquatic. It lives on insects and grubs and lays eggs. (Courtesy of the New York Zoological Society.)

marsupium; jaws are extended into a proboscis-like beak, and claws are adapted for digging.

Subclass Metatheria. To some extent the Metatheria, or Marsupialia, parallel the development of true mammals (Fig. 33). After a uterine development of 12 to 14 days the young are born in a precocious state and pass into the marsupium, where they remain attached to the nipples of the mother for 8 to 10 weeks.

In South America the several species of Metatheria include a small, mouse-like marine opossum and a strange little opossum shrew, *Caenolestes*.

In Australia the marsupials had free range since they evolved without competition from other mammals. Many converged in structure, habitat, and adaptations with the placental mammals of other lands. They developed into marsupial bears, wolves, moles, hyenas, cats, rabbits, and woodchucks. The dominant family, the kangaroos, represented by over a hundred species, ranges from giant plain dwellers to several small

arboreal species in which the forelimb is greater in length than the hindlimb and the tail is no longer the primary balancing organ.

The outstanding feature of the marsupials, as indicated, is the marsupium, or pouch. Associated with this is the precocious birth of the young and the consequent external attachment of the fetus to the mother.

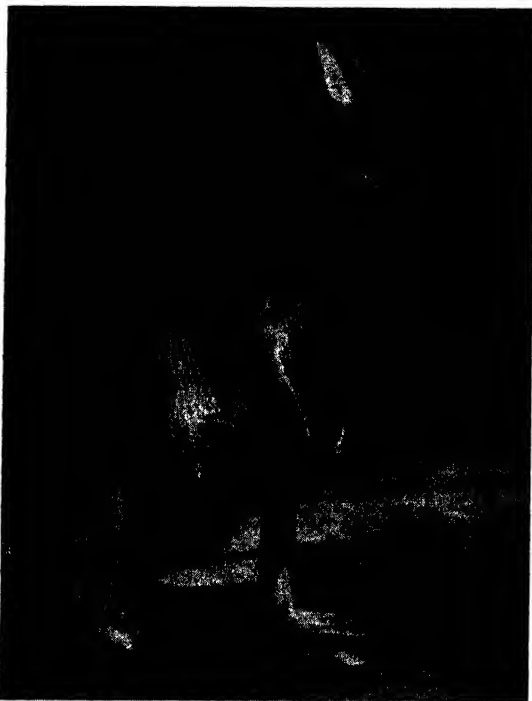


FIG. 33. The kangaroo *Macropus* is representative of the marsupial, or pouched, group of vertebrates. Some of the kangaroos are adapted to tree life. (Courtesy of the Philadelphia Zoological Garden.)

Subclass Eutheria. The placental mammals constitute the remaining backboned animals. At least 10 extinct and 10 to 15 living orders are identified. With some exceptions the Eutheria are adapted to land life. Cetacea and some Carnivora have taken secondarily to water, while the Chiroptera, or bats, are adapted to flight. Living Eutheria vary in type from primitive generalized edentates to dominant primates. In weight they range from 4-gm. shrews to 30,000-kg. whales. They

possess a relatively large brain in comparison with Prototheria and Metatheria; within the subclass great differences in brain size are correlated with differences in behavior. Highly developed sensory organs occur generally. The brain shows an increasingly large cerebrum, particularly in man, where it forms the greatest division. Complete separation of rectum and urogenital tract causes the cloaca to disappear in the adult. A placenta and true mammary glands provided with nipples occur in the females. In the forelimb of primates, considerable freedom together with change of function from that of body support to



FIG. 34. The elephant shrew, native of Africa, one of the insectivores, is shy and retiring in its habits. (U.S. Navy photograph. Courtesy of the Science Illustrated Magazine.)

that of grasping and manipulation exists. This freeing of the forelimb has apparently produced profound effects on the brain. Locomotor organs, highly specialized in ungulates, remain primitive and generalized in many others. The five-toed limb is an example of such generalized structure. Vocal apparatus is usually well developed. The larynx has evolved into an organ of speech in the genus *Homo*, and associated with this is the development of psychical life and of rational ideas.

Following are a few outstanding features of the individual orders of living Eutheria:

Order Insectivora: Shrews, Moles, Hedgehogs. These mammals are commonly retiring, nocturnal, and burrowing, or subterranean. They possess a five-toed plantigrade foot. Their dentition is generalized (Fig. 34).

Order Xenarthra: Armadillos, Sloths, Anteaters. Xenarthra originated in South America, where many fossil genera have been found. Teeth are lacking or poorly developed. The skin is scaly or horny. The feet are provided with claws. Food habits are insectivorous. In one genus of armadillo a peculiar division of the single fertilized ovum results in four complete embryos (Fig. 35).

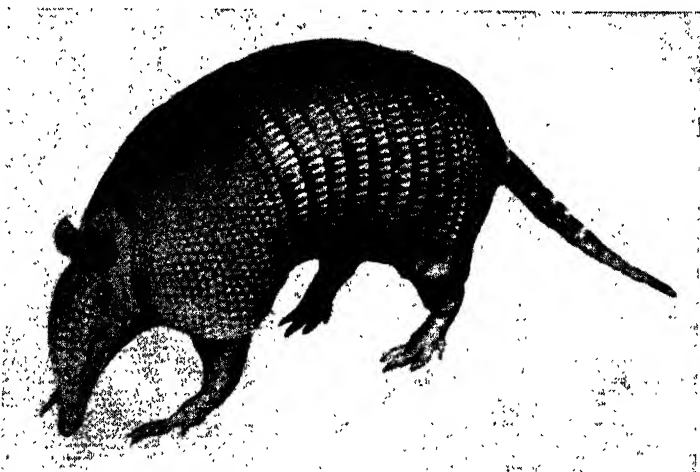


FIG. 35. The armadillo *Dasypus* wears an articulating armor. Its dentition is poor and is restricted to a single set of teeth. Quadruplets are usually developed from the fertilized egg.

Order Rodentia: Mice, Rats, Squirrels, Beavers, Rabbits, Capybaras, Guinea Pigs. These are usually small mammals with specialized gnawing dentition (Fig. 36). Their incisors grow throughout life, and canine teeth are absent. In diet they are herbivorous or omnivorous. The gestation period, during which several young develop, may be as short as 12 days. Included in the order are many nocturnal, burrowing, aquatic, and tree-dwelling types (Fig. 37).

Order Chiroptera: Bats. The forelimbs are adapted for flight; the digits are webbed and possess claws (Fig. 38). They are provided with a specialized sensory apparatus enabling them to avoid obstacles in flight. Certain vampire species are able to pierce the skin and suck blood. Chiroptera generally, however, are insectivorous and nocturnal, and they hibernate.

Order Dermoptera: Flying Lemurs. These gliding mammals have



FIG. 36. The squirrel *Sciurus*, one of the very active rodents, is developing considerable freedom of the forelimb. (*Photograph by John Warfel.*)



FIG. 37. The springhare, an African rabbit, has lost the use of the forelimbs for running and has developed a long tail.

extensive lateral skin folds uniting forelimbs and hindlimbs, enabling them to volplane from higher to lower tree levels. They are herbivorous and are restricted to the Malay Archipelago.

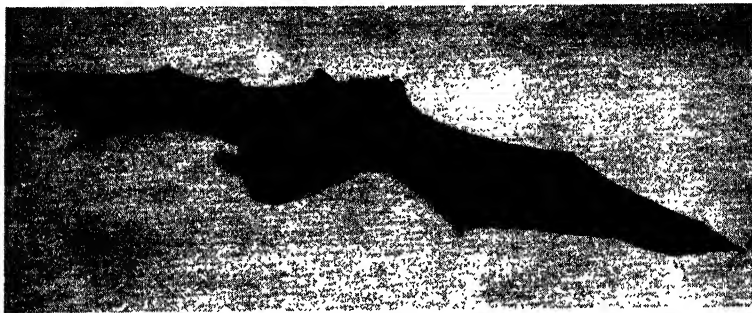


FIG. 38. The bat is a true flying mammal. Webs between the fingers of the forelimb have formed a membranous wing. The sternum is extended as a keel. (Courtesy of the Philadelphia Zoological Garden.)

Order Carnivora: Fissipeds and Pinnipeds. The fissiped carnivores include cats, bears, and dogs, among others; the pinniped carnivores include sea lions, seals, walruses (Fig. 39). Their dentition is specialized



FIG. 39. The lion, *Felis leo*, one of the largest of the cats, is characterized by power that overwhelms its victims. (Photograph from Smith.)

for shearing (carnassial teeth) and tearing (canine teeth). They are physically active and alert and have highly developed sensory organs. Claws of the fissipeds are frequently provided with a retractile mecha-

nism. The pinnipeds are aquatic carnivores with highly modified body appendages, adapted for swimming (Fig. 40). The brain is relatively larger in pinnipeds than in fissipeds.



FIG. 40. The seal is an aquatic carnivore completely adapted to marine life. Its brain is relatively much larger than is that of the land carnivores. *Lower left, brain; lower right, heart.* (Courtesy of the New York Zoological Society.)

Order Artiodactyla: Deer, Giraffes, Pigs, Cows, Sheep, Camels, and Others. The artiodactyls are even-toed, hoofed, and horned or tusked. Bunodont (cone-shaped) or selenodont (crescentic with ridges on the surface) dentition is present. Upper incisors and canine teeth are



FIG. 41. Thomson's gazelle, one of the even-toed ungulates, is one of the fastest of the land vertebrates. The adult carries elongate embossed horns.



FIG. 42. The zebra, *Equus quagga*, one of the odd-toed ungulates native to Africa, is difficult to tame. It appears to be the favorite diet of the lion. (Photograph from Anderson.)



FIG. 43A. The foot that imprinted this tread in soft earth was $23\frac{1}{2}$ in. long. It was the largest tread left by a herd of 128 wild elephants. The specimen to which the foot belonged was brought down and dissected after 12 days of tracking.

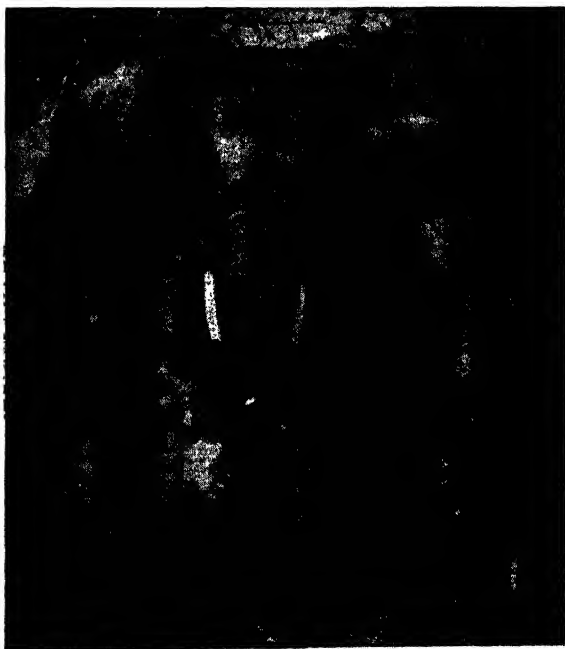


FIG. 43B. The African elephant, *Loxodonta africana*, is larger than the Indian proboscidian. Its ears are also relatively longer and wider. (Courtesy of the Philadelphia Zoological Garden.)

usually absent. They are herbivorous and ruminant (cud-chewing), and many have a four-compartment stomach (Fig. 41).

Order Perissodactyla: Horses, Tapirs, Asses, Rhinoceroses. Perissodactyls are odd-toed, digitigrade, herbivorous ungulates. Molars are commonly selenodont. The animals are usually large and are capable of rapid movement (Fig. 42).

Order Proboscidea: Elephants. There are two living genera of Proboscidea, *Elephas* of India and *Loxodonta* of Africa (Fig. 43A and B). The largest living land mammals, they are characterized by a long



FIG. 44. The African hyrax, or coney, is fairly plentiful in certain regions of southeast Africa. (Courtesy of the Philadelphia Zoological Garden.)

proboscis and great ears. The tusks are specialized incisor teeth. The gestation period of about 20 months terminates with the birth of one offspring.

Order Hyracoidea: Hyraxes. These are small mammals about the size of guinea pigs. They are herbivorous and rock-dwelling (Fig. 44). Their lophodont (ridges on the crown) dentition places them in close relationship to the ungulates.

Order Sirenia: Manatees and Dugongs. The Sirenia are marine inhabitants although they frequent fresh-water inlets and bays. They are slow-swimming, herbivorous mammals with pectoral mammae, a horizontal tail fin, lophodont dentition, and extremely small eyes and brain (Fig. 45). The pectoral fins are modified as paddles. The dia-

phragm is greatly elongated, extending to the pelvis, and the intestine may exceed 100 ft. in length.

Order Cetacea: Whales, Dolphins, Porpoises. The whales are subdivided into two suborders, the toothed whales, or Odontoceti, and the



FIG. 45. The manatee, representative of the Sirenia, is a vegetarian, feeding on sea grasses. The diaphragm extends horizontally from the pectoral girdle to the pelvis, dividing the celom into a dorsopleural and a ventroabdominal cavity.

whalebone whales, or Mystacoceti. In the latter, teeth have been replaced by whalebone. The Cetacea are sea mammals with cylindrical bodies whose appendages have evolved into flippers (Fig. 46). Nostrils on the dorsum of the head serve as blowholes for breathing. The

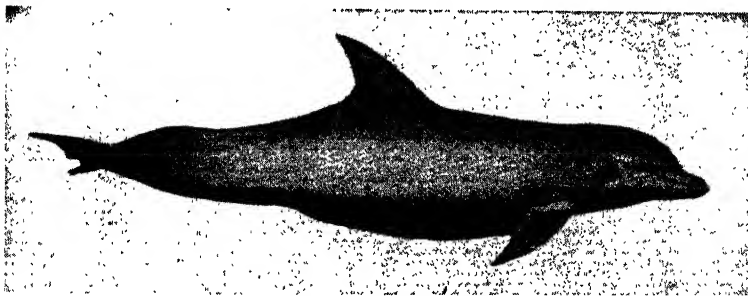


FIG. 46. The porpoise *Phocaena*, a toothed cetacean, is one of the swiftest marine inhabitants.

larynx has completely lost its connection with the mouth. Mammary glands lie in pockets lateral to the anal aperture. The horizontal tail fin may have a width of 20 ft. or more, and pectoral flippers may exceed 22 ft. in length. The body weights of these greatest of mammals may exceed 200,000 lb.

Order Primata. Three subdivisions are recognized among primates:



FIG. 47A. The New World monkey, *Aotus zonalis*, is a small, shy creature adapted to nocturnal activities.



FIG. 47B. The chimpanzee *Trogodytes* has many structural characteristics in common with man. The specimen pictured was taken in the great Budonga Forest in Uganda, Africa.

(1) Tarsioidea, or sceptor monkeys, found in the Malay Peninsula; (2) Lemuroidea, in Africa and Madagascar; (3) Anthropeidea, Old and New World monkeys (Fig. 47A), the great apes, and man. The apes include the gibbons, orangutans, chimpanzees, and gorillas (Fig. 47B). Of these the gibbons and orangutans are Asiatic in distribution, while the chimpanzees and gorillas are African. Originally all members of the order were tree dwellers. With the exception of man they remain forest dwellers. The gorilla no longer nests in trees, and the chimpanzee and baboon are active on the ground, although they live in trees at night. The group has stereoscopic vision, five digits on each hand and foot, generally with nails, and an opposable thumb and commonly opposable great toe. Old and New World monkeys have tails; in the New World monkeys these are prehensile. Old World monkeys, apes, and man are characterized by 32 permanent teeth, New World monkeys by 36. The food habits of monkeys and apes are herbivorous and frugivorous; of man, omnivorous. In man, voice, language, the ability to reason, and a rich psychical life have evolved.

SUMMARY

The term "classification" remains an abstraction to many of us. We recognize a grasshopper and distinguish it from a cricket. We identify a horse and note differences between it, a donkey, and a zebra. We make much of differences in color in the human race, to the extent of passing drastic laws based on pigmentation. Biologic classification, however, carries many implications which go far beyond these superficial observations, since it helps to explain underlying relations.

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CHAPTER 3

THE INTEGUMENT

INTRODUCTION

The integument, like the other systems of the body, undergoes an evolution from *Amphioxus* to man. It is an index of the scale of being, just as are the nervous and circulatory systems. It differs from species to species in minute detail; yet it embodies basically similar features in the great assemblage of vertebrates.

The skin, or outer covering, of an animal is the limiting membrane separating it from chaos, marking the individual off in space from other living entities. In the vertebrates this covering is of two basic layers, an outer *epidermal* coat derived from ectoderm embryonically, and an inner *dermal* coat derived from mesoderm. Subcutaneous connective tissue ties the dermal layer to the underlying fascia. Scales, feathers, hair, pigmentation, nails and claws, hoofs and horns, which appear in one or the other or both of the integumentary layers, are skin derivatives.

FUNCTION

A basic and natural function of the skin is protection. This is achieved in various ways—by toughness of the outer skin, which may be provided with a cuticle, or through thickening of the inner layer to provide a hide, or by sensory endings and organs. Secondary structures like scales, feathers, bony plates, and hair represent further expansions of the protective function.

The natural forces under which animals have evolved have been responsible for another group of protective skin derivatives. These are claws, nails, hoofs, and teeth. Their protective function is obvious. Without claws the powerful Carnivora, as we find them today, could probably never have reached their present state. Such structures must not be thought of as mere passive instruments, for they have passed far beyond this stage and have become highly specialized mechanisms for maiming and killing.

Sweat glands and capillary beds for regulation of body temperature in warm-blooded animals are protective devices. Temperature regulation, vitally significant to these animals, compels heat conservation at

certain times and heat dissipation at others; the latter may be increased by sweat, which cools the skin on evaporation, while conservation is accomplished by reducing capillary blood circulation in the skin bed.

The skin protects against bacterial invasion as well as against animal attack. This is achieved in part by its impervious structure or through secretions of specialized cells. Such cells may secrete mucus of evil taste to which may be added poisonous qualities. More subtly, it protects through specialized sensory nerve endings plentifully and strategically distributed through the integument. Touch, pain, temperature, and chemical receptors, eye, ear, and nose are sensory specializations, which in effect extend the limits of the body to any distance from which it may be stimulated. Thus a giraffe that sights the hunter 2 miles away has effectively extended its body and its protective zone for that distance. All such sensory structures are adaptations enhancing the chances for survival.

The skin functions cited above protect the individual; certain others protect the species since they serve as lures to stimulate reproduction. Periodic changes in perincal skin color in female mandrills and in some other monkeys are correlated with sexual receptiveness of the female. The converse of this pattern is seen in the brilliant plumage of many male birds: the color of the strutting peacock or barnyard cockerel undoubtedly helps to induce submission in their hens. Scent, too, emanating from specialized skin glands in many land vertebrates, provides powerful sexual stimuli. While man's aesthetic nature attempts to substitute exotic perfumes for these more obvious glandular scents, the latter continue their role as sexual excitants.

All these life-conserving functions have been built into an epithelial covering originally of great simplicity, although even in the lowly invertebrate coelenterates the labile epithelium has already taken on a variety of activities that mediate between environment and organism.

It was stated earlier that the skin has two basic layers, an outer epidermis and an inner dermis, or corium, the former of ectodermal, the latter of mesodermal origin. The skin does not retain this simple state except in the protochordate urochords, hemichords, and cephalochords. In the remaining chordates the epidermis becomes stratified.

THE SKIN IN THE CHORDATE CLASSES

Urochords. The urochords possess an epidermis of a single layer of flattened epithelial or columnar cells. Interspersed among the epithelial cells are many glandular cells. In the Appendicularia, minute free-swimming tunicates, a mucous secretion supplied by these unicel-

lular glands to which chance edible particles or small organisms may adhere serves as food for these animals (Figs. 48, 49). A thin cuticle is secreted by the epidermis. In the *Ascidia*, which pass through a free-swimming larval stage followed by metamorphosis and a sessile state, the epidermis secretes a cellulose-like outer test of tunicin. The

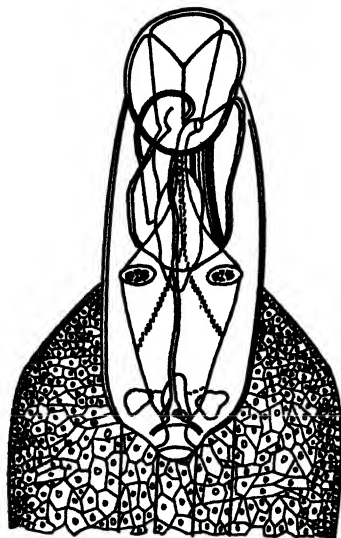


FIG. 48A. Appendicularia, *Oikopleura albicans*. Anterior end of body, dorsal view. Pavement-like single layer of epithelium forming a polyhedral mosaic body covering. Cells become smaller on the sides of the body. (After Fol and Lohmann.)

test contains mesodermal, pigment, and ameoboid cells. It may be clear and hyaline, or fibrillar with circulatory channels running through it. The dermis, or corium, is of loose, fibrillar connective tissue.

Hemichords. The skin of the hemichords shows its primitive state by the retention of covering cilia. The epidermis is a single layer of epithelial cells, many of them glandular. The latter provide a viscous secretion to which sand grains adhere to form temporary tubes which house these worm-like animals. The underlying corium is a loose, fibrillar connective tissue.

Cephalochords. *Amphioxus* likewise has a two-layered skin, an outer epidermis of a single layer of columnar epithelial cells over a dermis of compact connective tissue (Fig. 50). The pigmented epidermis secretes a porous cuticle. In the region of the mouth cirri it may be ciliated, or provided with sensory hairs. Sensory cells are interspersed among the covering epithelial cells. A subcutaneous connective-tissue layer, containing

blood vessels and nerve endings and strengthened by connective-tissue strands, underlies the dermis.

Cyclostomes. A stratified epidermis first occurs in the cyclostomes, which comprise the *Myxinoidea*, or hagfishes, and the *Petromyzonoidea*, or lampreys (Figs. 51, 52). This is made up of a living basal layer, the stratum germinativum; superficial to this the cells take on a flattened, or squamous, shape. Reminiscent of the invertebrate skin, a secreted

cuticle covers the squamous layer. Numerous pigment, gland, and sensory cells are distributed in the epidermis. Another feature of the hagfish skin is the great number of mucus-secreting glands in the epidermal layer. These may be single goblet cells or multicellular glands.

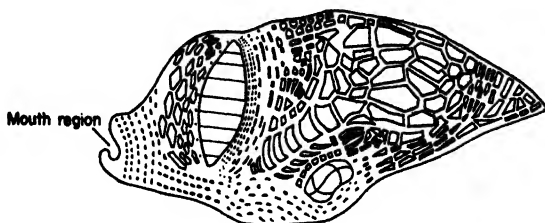


FIG. 48B. Appendicularia, *Oikopleura vanhoffeni*. The peculiar glandular surface epithelium (oikoplast) is a mosaic of plasma-containing cells. These secrete a transparent cuticle. (After Lohmann and Buchmann.)

The skin of the lamprey, while slimy, is not so well supplied with mucous glands. In these cyclostomes, specialized, elongate, cob-like cells in contact with the basal layer of epidermis extend well into the corneal layer of the outer skin. Horn teeth of the cyclostomes are cornified epidermal derivatives.

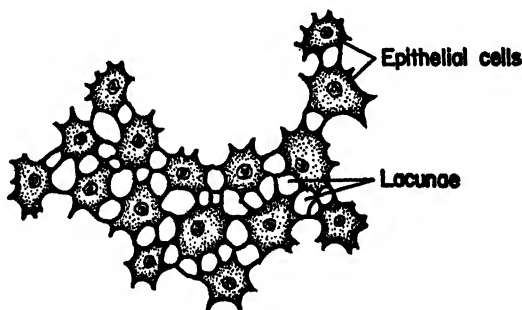


FIG. 49. Ascidiacea, *Boltenia echinata*. Surface epithelium with lacunar spaces between cells. (After Saint Hilaire and Huns.)

The corium underneath the epidermis is a compact connective-tissue layer developed from the mesoderm, but it produces no specialized derivatives in this group.

Fishes. Skin. The fish skin bears considerable resemblance to that of the cyclostomes (Fig. 53A, B). The epidermis is stratified, with pro-

gressive flattening of cells toward the surface, but cornification as it appears in the epidermis of land animals does not occur. This outer skin layer is well supplied with mucous glands which in some species secrete poison.

The corium, made up of a loose outer and a deeper, more compact

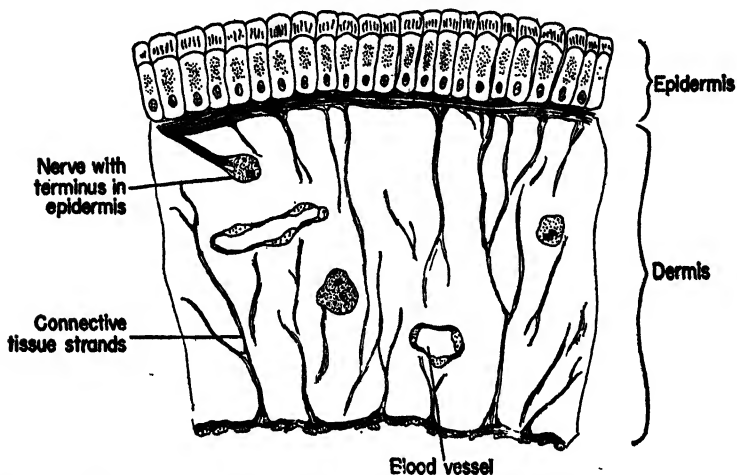


FIG. 50. Skin of *Amphioxus*. The epidermis of *Amphioxus* is a single layer in thickness. The underlying connective tissue corresponds to the dermis of the vertebrates.



FIG. 51. Cyclostome, *Lampetra fluviatilis*. Cross section through skin, showing epidermis, corium, and subcutaneous layers. (After Krause and Pietschmann.)

layer, frequently has chromatophore cells, presumably of protective value. Pigment is distributed in granules in these cells, and rapid expansion and contraction of these elements produce the characteristic color changes. These pigment cells may migrate into the epidermis.

Dermal Derivatives. An outstanding dermal development in the fishes is the scale. This originates from dermal papillae, with contributions from the epidermis in some types of scales, as will be shown.

Scales are of various types; cartilaginous fishes are protected by placoid scales, while bony fishes are covered with flattened cycloid, ctenoid, or rhomboid scales. (Fig. 54).

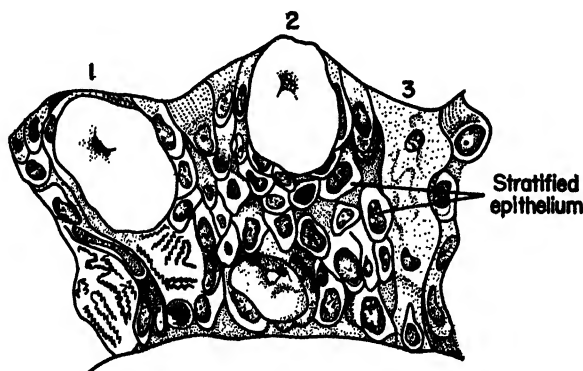


FIG. 52. Cyclostome, *Myxine glutinosa*. Section through epidermis. Notice stratified epithelium. (1) Mucous cell approaching surface. (2) Mucous cell at surface about to discharge. (3) Empty mucous cell. (After Schreiner and Pietschmann.)

The placoid scale is of dual origin. The hard enamel-like covering of the spine arises from the epidermis; the dentinal base, body of the spine, and the pulp, from the corium. The flattened rectangular base is embedded in the skin, and from it the spine protrudes through the surface. The spine has a hollow center continuous with an opening in the base, comparable with the pulp cavity of a tooth. The blood and nerve supply enters through this cavity. A vitreodentinal, or outer layer, of the spine is secreted by the epidermis after the scales are formed in the corium and before they erupt. Until recently this was erroneously considered the enamel layer. From this placoid scale the vertebrate tooth has apparently evolved, since in manner of origin and the appearance of vitreodentin, dentin, and pulp cavity the two show homologies.

Ganoid scales are rhomboid plates joined with each other at their margins (Fig. 22). In the gar pike they form a complete vestment for the body. Developed entirely from the corium, they possess a hard outer surface, the ganoin, and a deeper layer of isopedine, or lamellated bone. Ganoin lacks a cell structure and bears a superficial resemblance to enamel. Isopedine contains bone cells and is superficial to ordinary

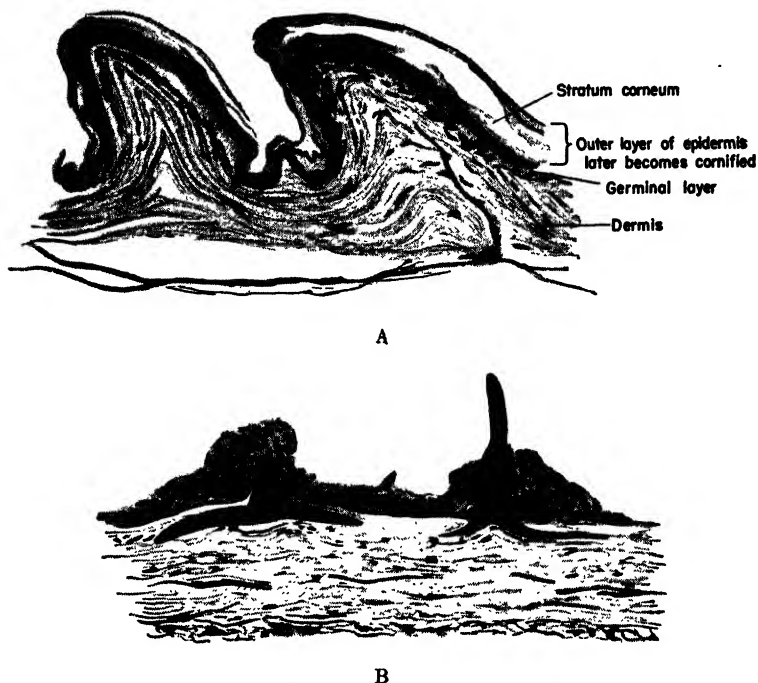


FIG. 53. A, section through skin of monitor lizard. B, section through dogfish skin, showing the position of the placoid scales with relation to the epidermal and dermal layers.

bone. Haversian canal systems similar to those of the skeleton push through both layers of the scale, and in those ganoid fishes with dermal spines the haversian canals enter these structures. These canals are provided with blood vessels which supply the scales and spines.

A modification of the ganoid scale, known as the cosmine type, is found in the extinct crossopterygian fishes. The scale consists of an outer dentinal layer, a middle, vascular bony one, and an inner layer of isopedine, or lamellated bone.

Cycloid scales overlap at their outer margins, permitting great flexibility to the body covering (Fig. 54C). They are circular, and their growth is at the periphery. Since growth is seasonal, especially in many fresh-water fishes, the concentric growth rings make it possible to determine the age of the fish. The cycloid scale is developed from the

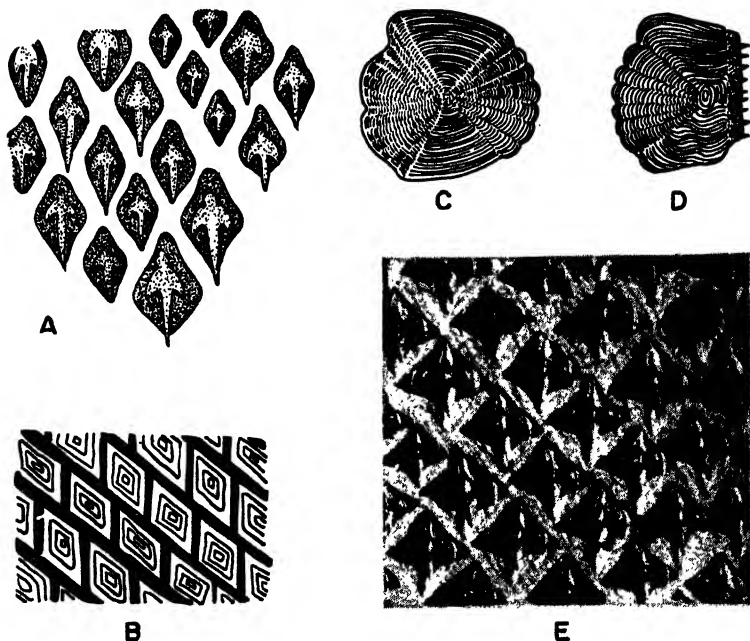


FIG. 54. A, arrangement of the placoid scales in sharkskin. B, the rhombic plates constituting the pavement-like skin of the ganoid fishes. C, the cycloid scale present in the Dipnoi is characterized by growth lines and serrated margins. D, the ctenoid scale typical of most bony fishes has its free margins covered by fine, tooth-like spines. E, detail of placoid scale in sharkskin. (E, Courtesy of the General Biological Supply House, Chicago, Ill.)

corium. Its outer layer consists of bone cells; the underlying lamella is of calcified connective tissue.

The ctenoid scale, a modification of the cycloid, is found in many teleost fishes (Fig. 54D). It has two lamellae, or layers, an outer one of bone with definite cellular structure and an inner one of fibrous connective tissue, partly calcified. The free posterior margin of the scale is toothed, or pointed, hence its name. The free surface is generally

covered with pigmented epidermis. The anterior margin of the scale, embedded in the integument, is fluted or serrated.

Spines, common to many cartilaginous and bony fishes, are of two types, *keratin* spines derived from the corium and found in many elasmobranchs and *bony* spines of epidermal origin in the bony fishes. The latter develop in the region of the dorsal fin from the germinative layer of the epidermis, and during growth they sink deeply into the integument. They originate from two centers, one on either side of the midline, and

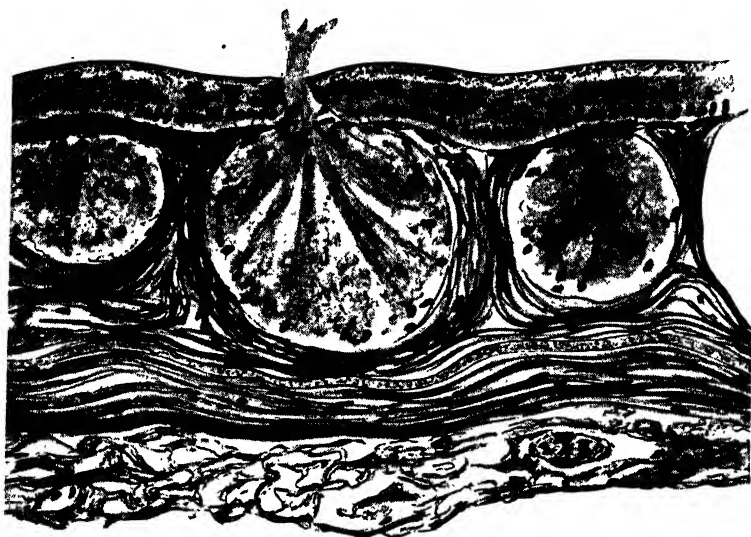


FIG. 55. The skin of the frog is characterized by many mucous glands that open on the surface. The dermis has an outer, loose connective-tissue layer and a deep, compact one. (After Ihle.)

in their upward growth they fuse and form the typical middorsal spines. They articulate with receding cartilaginous or bony fin rays, and by appropriate muscle action raising and lowering of the median fin is brought about.

Amphibia. Skin. The skin of the amphibians forms a loose vestment, in contrast to the tight-fitting integument of the fishes (Fig. 55). This is characteristic of land animals generally, with the exception of the reptiles.

The aquatic larvae of all existing amphibians are ciliated; after metamorphosis the cilia are lost, and a thin secreted cuticle covers the

epidermis. The epidermis is stratified and is proliferated from its deepest layer, the stratum germinativum. The corneum, or outer layer of this stratified epidermis, is shed periodically in many amphibians. Warts, common in toads, represent cornification of the epidermis.

The corium has an upper layer of loose connective tissue and a deeper compact layer. It contains the blood supply, innervation, and bodies of the mucous glands, with which amphibia are generously supplied. Lymph spaces underlying the corium account in part for the looseness of the amphibian skin and make its removal easy.

Mucus secretion in the Amphibia is perhaps best developed in Necturus, and if, for example, a living specimen is firmly grasped, sufficient mucus may be discharged to enable the animal to wriggle free in a few moments. Apparently such secretion is an adaptation against drying as well as a protection from enemies. In some amphibians it has poisonous qualities. In many the skin takes on a respiratory function following metamorphosis. This is particularly true of the lungless salamanders, where the gills are absorbed in metamorphosis and lungs fail to develop.

Dermal Derivatives. Amphibians generally are without scales. The extinct stegocephalians, however, from which the Amphibia presumably arose, had well-developed plates of corneal origin over the abdominal regions. In living *Gymnophiona* (naked amphibians), scale clusters derived from the corium are buried in the skin in conjunction with poison glands. These scales consist of rings of small platelets forming a hard surface, held together by a dense, underlying connective-tissue layer. The wart-like structures appear in some toads, as mentioned, and thickened areas may also develop in the corneum on the thumbs of males, associated with the clasping function.

Claws in the vertebrates first appear in the Amphibia and occur on the posterior extremities of a few genera, namely, in the South American toad *Xenopus*, the frog *Hymanochirus*, and the tailed *Onchodactylus*. They are a cornification of the corneal epidermal layer, just as are the hoof and nail. In amphibians, reptiles, and birds the claw is a cone-like terminus for the digit in contrast to the mammalian nail, which is dorsal in position.

Reptiles. Skin. The reptilian skin varies greatly in different orders. In the crocodiles, it is a heavy armor; in turtles, besides this armor, bony plates of mesodermal origin are added underneath the skin derivatives (Fig. 56). In snakes, ventral scales are modified for locomotion; in lizards, generally, the skin is thin and flexible, although provided with scales. Characteristically, the reptilian epidermis and the resulting

horny tissue may be shed. Thus a sloughed snake skin is not an uncommon sight in regions where these reptiles are plentiful. The corneum, or outer division of the skin, is derived from the deep, living stratum of the epidermis, the germinative layer.

The corium, or dermal layer, underlies the epidermis and has a dense outer portion which becomes hardened and bone-like in the crocodilia. In lizards it is heavily pigmented through chromatophore cells, which make possible rapid color changes as in the chameleon. The deeper

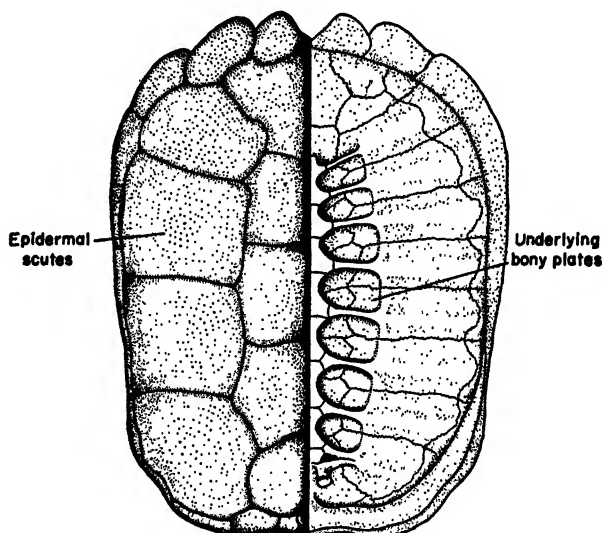


FIG. 56. The carapace of the turtle has an outer layer of thin epidermal scales overlying heavier bony plates of dermal origin.

part of the corium is a loose connective tissue in which fat may be stored. The blood and nerve supply extends into the corium, but not into the epidermis.

The reptilian skin is further distinguished by absence of mucous glands, although specialized scent glands are common to turtles, snakes, and crocodiles.

Dermal Derivatives. Epidermal scales and horny shields, or scutes, appear in a number of reptilian orders. In lizards and snakes scales are plentiful; in turtles they overlie the bony plates of dermal origin, and in crocodiles bony plates are embedded in the skin underneath the epidermal ones. Embryonically these appear at the sites of the dermal

papillae. Above these papillae the stratum germinativum proliferates corneal cells, which become flattened and compressed and which overlap. In sloughing its skin the snake sheds the entire corneal layer, which generally separates from the deeper portions of the epidermis in one piece.

Commonly in reptiles the scales covering the upper surface of the head are greatly modified and form shields of close-fitting armor over the skeletal structure. In the snakes also, the scales are modified over the ventral surface of the body to form rows of transverse shields. These, held together with specialized muscles, supply the locomotor apparatus.

The armor of the turtle, already noted, consists of a dorsal *plastron* and a ventral *carapace*, the two joined by lateral bridges. This armor has an outer layer of horny plates, or scutes, of epidermal origin and an inner dermal layer of bony plates. Ribs and vertebrae underlying these plates become fused, forming an inflexible foundation for the equally rigid dermal and epidermal layers of the armor.

In the crocodiles epidermal plates are embedded in the skin. Under these are dense dermal connective-tissue pads, which become ossified in the dorsal regions. Other specialized dermal and segmental ossifications on the ventral side are the *gastralria*, or abdominal ribs (Fig. 80). Independent of true ribs, they represent protective adaptation for the ventral surface, since the low-slung bodies of these long, heavy reptiles are in frequent contact with the earth. Gastralia are absent in snakes, where ventral protection is offered by well-developed transverse shields. Epidermal claws for digging and defense occur on the tips of all digits in all save the limbless reptiles.

Horny beaks, like claws, are of epidermal origin. In turtles, teeth have been replaced by beaks, although primordial teeth are laid down in the embryo but fail to erupt. The beaks extend over the free margins of maxilla and premaxilla of the upper jaw and over the dentary bone of the lower, forming sharp cutting edges.

Birds. Skin. In contrast to the heavily armored skin of many reptiles, that of the birds is thin and poorly adapted for protection except secondarily through feathers and subcutaneous fat (Fig. 57). The epidermis is stratified, with a cuboidal or columnar germinative layer. Its cells become progressively flatter as they approach the surface, where they give rise to a distinct corneal layer from whose surface squamous cuticular cells are constantly shed. The corium is loose connective tissue in which fat is stored, particularly in aquatic and arctic birds. In its dense outer stratum are smooth muscles which raise the feathers.

In the head and neck region the naked corium may be highly vascularized, as in the specialized comb and wattles of the common fowl and the red neck of the turkey and the buzzard. The skin of birds is without glands, except for the pygeal body at the base of the tail and the sebaceous glands in the ear canals of some fowls.

Dermal Derivatives. Scales are confined to the feet and legs and, as in reptiles, are derived from epidermis and dermis (Fig. 58*B, C*). Feathers appear to be derivatives of scales, although the transition from scale to feather has not been observed. Similarity in origin of the two structures is the only connecting link between them.

Claws in reptiles and birds occur on the tips of all digits. In reptiles they are used for digging and defense; in birds, for scratching or, in

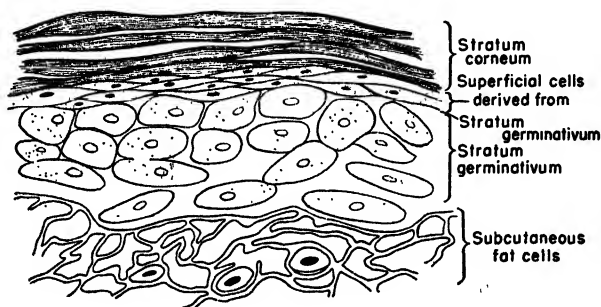


FIG. 57. The bird skin. The integument is characterized by thin epidermis and dermis covering a thicker subcutaneous layer, where fat may be stored.

conjunction with the digits, for holdfasts in perching. In carnivorous birds they appear as talons and aid in the capture of prey. Spurs, frequent in certain male birds and similar in origin and structure to claws, are supported by bony outgrowths from the leg bones. Like claws, they represent a cap over an underlying core of bone. Their function in combat is obvious.

The beak, as in reptiles, is of epidermal origin and assumes a variety of shapes and curvatures (Fig. 58*A*). In ducks and geese, which feed in mud, the beak is broad and flat. In tall wading birds like the heron it is elongate and conical. In the curlew the long beak curves upward gracefully; in the godwit it arches downward. In the African hornbill and in the South American toucan it is of enormous proportions, making a grotesque caricature of the head. In the cross-beaked flycatcher with the significant name of *Loxia curvirostra curvirostra*, the tips are crossed. In the Arctic puffin the bill undergoes curious changes during the breed-

ing season, becoming partly overlaid by cornified tissue, which is lost during the sexual resting period. In some parrots tooth-like serrations appear at the edges, although they are not related to true teeth. Tooth ridges have been found in the merganser, tern, gallinule, ostrich, and others. These originate as epithelial swellings on the jaws but fail to erupt and sink into the mesoderm.

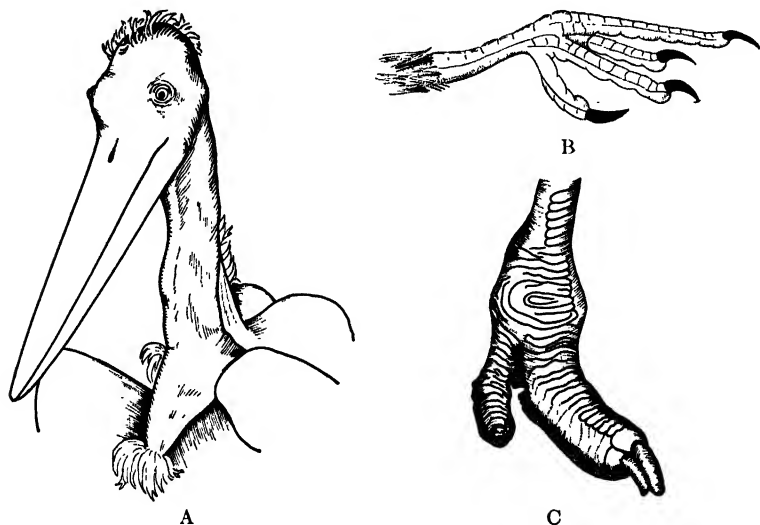


FIG. 58A. The beak of the marabou stork, like that of other birds, is a horny (epidermal) sheath incasing the elongate upper and lower jaws.

FIG. 58B. Horny scales are retained on the foot of the bird, identical with reptilian scales. The digits terminate in pointed claws. (After Messer.)

FIG. 58C. The ostrich foot terminates in two toes, as compared with three in the South American rhea and four in most of the remaining birds. Scales are retained over the dorsum of the foot.

Feathers are skin derivatives arising from dermal papillae and from the germinative epidermal stratum above the papillae (Figs. 59, 60). Three types occur: *down feathers*, or plumules, *contour feathers*, or plumae, and *hair feathers*, or filoplumes. The down feather is characterized by a quill, barbs, and barbules. It develops as follows: When the feather papilla has been established, the germinative layer of the epidermis grows upward to form the finger-like *quill*, which pushes through the skin. The core of this projection is of dermal origin and provides nourishment. The corium, which has grown into the

projection, is arranged in a series of longitudinal ridges or columns covered by epidermis. At the base of the feather the germinative layer grows downward to form the *feather follicle*. At the termination of growth, the vessels supplying the follicle atrophy, and the outer epidermis dries; the pulp is changed into *pith*, releasing the columns formed by

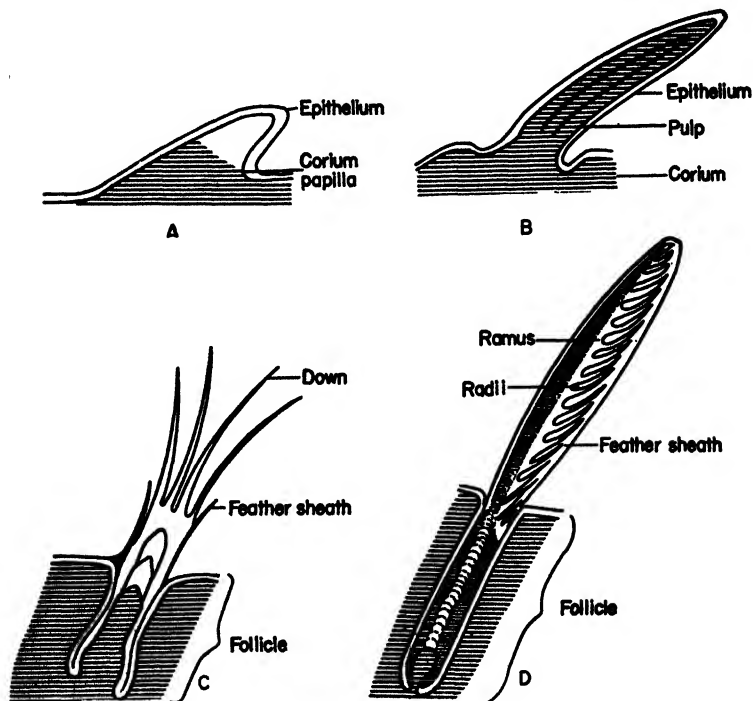


FIG. 59. The feather is developed from the epidermal and dermal layers of the skin. The down feather terminates in several hair-like endings (A, B, and C). The contour feather, of similar origin, terminates in a series of interlocking barbs and barbules resulting in a vane, D. (Modified from Ihle.)

the corium. These are the *barbs*. They occur at the top of the quill, and small *barbules* appear on the sides of the barbs. These feathers form the down of young nestlings and the undercoat of arctic and aquatic birds.

A contour feather consists of a *shaft* and a *vane*. The base of the *shaft*, the *quill*, is embedded in the follicle. This end is open and forms the lower *umbilicus*. On the ventral surface of the quill, at the level of

the lower margin of the vane, is a second opening, the *upper umbilicus*. An *aftershaft*, or accessory feather, develops at the upper umbilicus. The vane extends on either side of the shaft and is made up of barbs, from which pass barbules with hooks at their sides and tips that interlock with projections from adjacent barbs. The result is a firm, unbroken surface, necessary for flight.

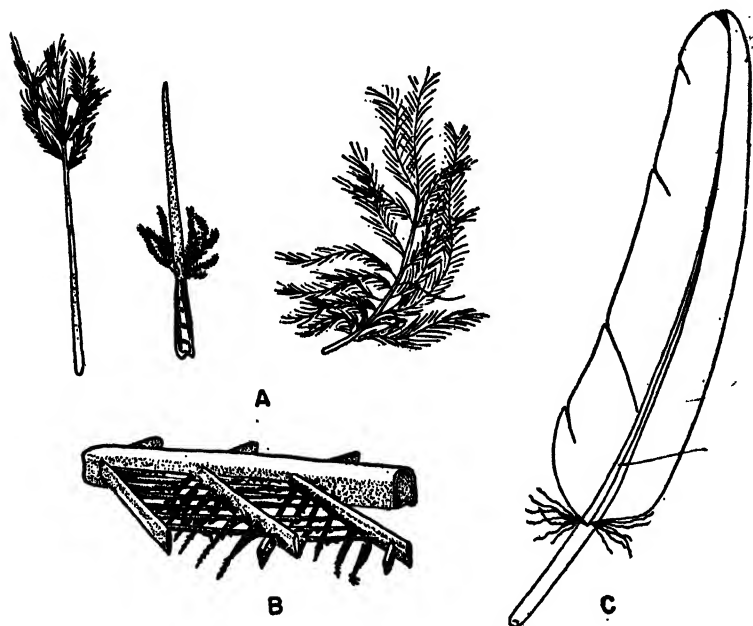


FIG. 60. A, detail of down feathers and filoplumes; B, detail of interlocking barbules; C, shaft and vane of a contour feather. (A and B after Storer. C after Messer.)

The contour feather arises in much the same manner as the plumule, save that the corium of the papilla grows out into oblique rods from the middorsal part of the future shaft. These diagonal rods form the barbs, while the undivided portion is retained as the shaft. When the epidermis dries, the rods separate into individual barbs but remain attached to the shaft. They are joined to each other through the barbules.

Hair feathers are either primitive or degenerate feathers. They

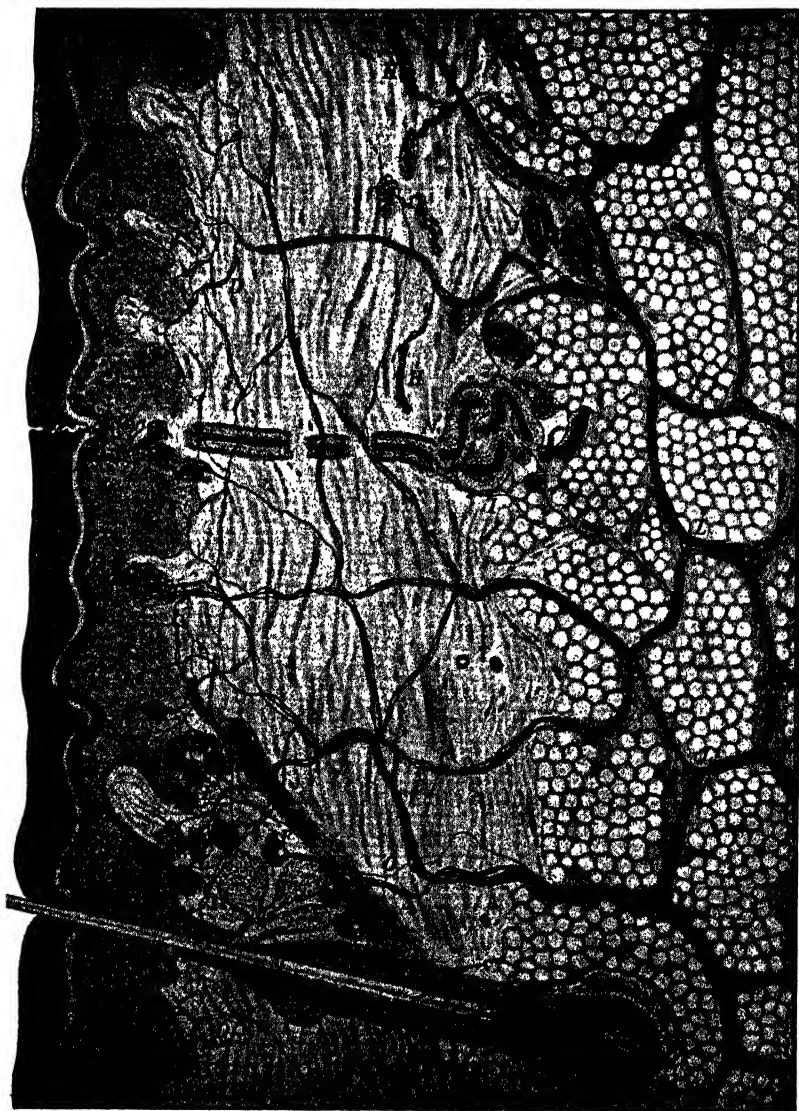


FIG. 61A. The mammalian epidermis has several strata which originate from the living stratum germinativum. Nerve endings and capillaries terminate in the dermal layer. *A*, touch discs (Merkel); *B*, free endings (pain); *C*, touch corpuscles (Meissner); *D*, nerve fibers (pain); *E*, end bulb (cold—Krause); *F*, nerve

originate from a feather papilla and possess a small, hair-like shaft with a few barbs at the tip; others may have a vestigial vane, or they may be without vane or barbs.

Mammals. Skin. Outstanding features of the mammalian skin are the thick dermal layer, furnishing the leather of commerce; the variety of glands, which may be sebaceous, sweat, or mammary; and hair or fur (Fig. 61A, B).

The living layer of the epidermis, the *stratum germinativum*, gives rise to a distinctive *stratum granulosum* of granular cells undergoing

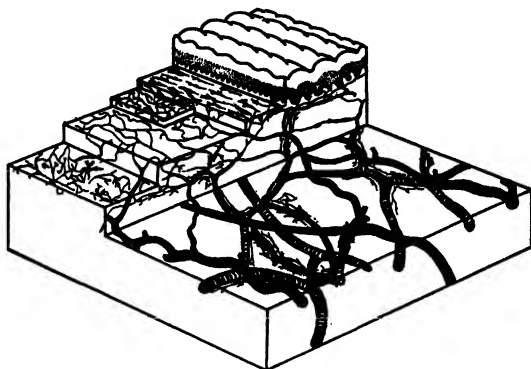


FIG. 61B. Blood supply to the skin. The blood passes from subcutaneous tissue to the dermis and nourishes the germinative layer of the epidermis from underneath. (After Spalteholz.)

degeneration. These changes result in a well-defined, clear hyaline layer, the *stratum lucidum*, external to the granulosum.

External to the *stratum lucidum* the thick *corneal layer*, so characteristic of mammals, appears. Near the surface these corneal cells undergo progressive flattening, resulting in the scale-like squamous layer. This is worn away constantly and is not sloughed in periodic molting as in the reptiles, for example. The germinative stratum presents a ridged outline produced by the *dermal papillae*, which push into this region from below and contain blood vessels and nerve endings to supply the germinative layer of the epidermis.

endings (warmth—Ruffini); *G*, nerve endings on hair-follicle (touch); *H*, pressure endings (Ruffini); *I*, sympathetic nerve fibers to sweat gland; *J*, Pacinian corpuscles (pressure); *K*, Golgi-Mazzoni pressure endings; *L*, bundles of nerve fibers; *M*, sebaceous gland; *N*, sweat gland; *O*, sympathetic nerve fibers to arrector pili muscle. (Courtesy of the Journal of Anatomy.)

The dermis varies in thickness in different mammalian species. It has an outer *papillary layer*, already noted, which joins the germinative stratum of the epidermis, and a deeper *reticular layer*. The latter is a dense, felted connective-tissue sheet, which when tanned becomes leather. Pigment cells, nerve endings, and capillaries occur in the derma. In certain areas of the derma, smooth muscles appear in a net-like layer, *e.g.*, nipples, scrotum, penis. In addition to the sebaceous, sweat, and mammary glands the mammalian skin may contain special scent glands.

Dermal Derivatives. Scales are found in a number of mammals, particularly in the scaly anteater and the armadillo. In the latter they are of epidermal origin, supported by underlying dermal papillae. Scales and plates are arranged in nine bands over the back of the armadillo. The front segment of this armor constitutes an anterior shield and the back the posterior shield. The bands are held together by the tough connective tissue of the corium. Scales also are retained on the tail of the opossum, certain rodents, and insectivores.

Although there is no direct evidence that hair originates directly from the scale, the two are closely related embryonically.

Among mammals, claws, hoofs, and nails are variously developed, but one or the other is always present (Fig. 62). In carnivores, the claws are outstanding. Here they become effective weapons in conjunction with agile and powerful limbs. Actually they are highly specialized mechanisms for killing. Muscles that attach to the terminal phalanges make it possible to extend or sheath the claws at will.

The hoof. The hoof is a modification of the claw. In digitigrade animals, which stand on the tips of their toes, it is terminal and characterized by great expansion of the nail, or unguis, which completely surrounds the subunguis. This subunguis is not to be confused with the frog, a tough tissue on the underside of the foot which partly absorbs the shock when the foot strikes the earth. Hoofs may be odd or even in number. Ungulates with even-numbered toes are Artiodactyla; those with odd are Perissodactyla.

The nail. Nails are characteristic of the Primates, although in the lemurs, tarsioids, and South American Midas monkeys the transition from claw to nail is incomplete. In lemurs the second digit of the foot retains a claw, and the remaining digits carry nails. This claw is used as a comb in arranging the fur. In the primitive Midas monkeys and in *Tarsius*, the specter monkey, claws are retained except on the thumb. The chief distinction between claw and nail is the lessened curvature of the latter. The nail is expanded laterally and is thinner and less tough than the claw. A very narrow subunguis joins the under surface of the

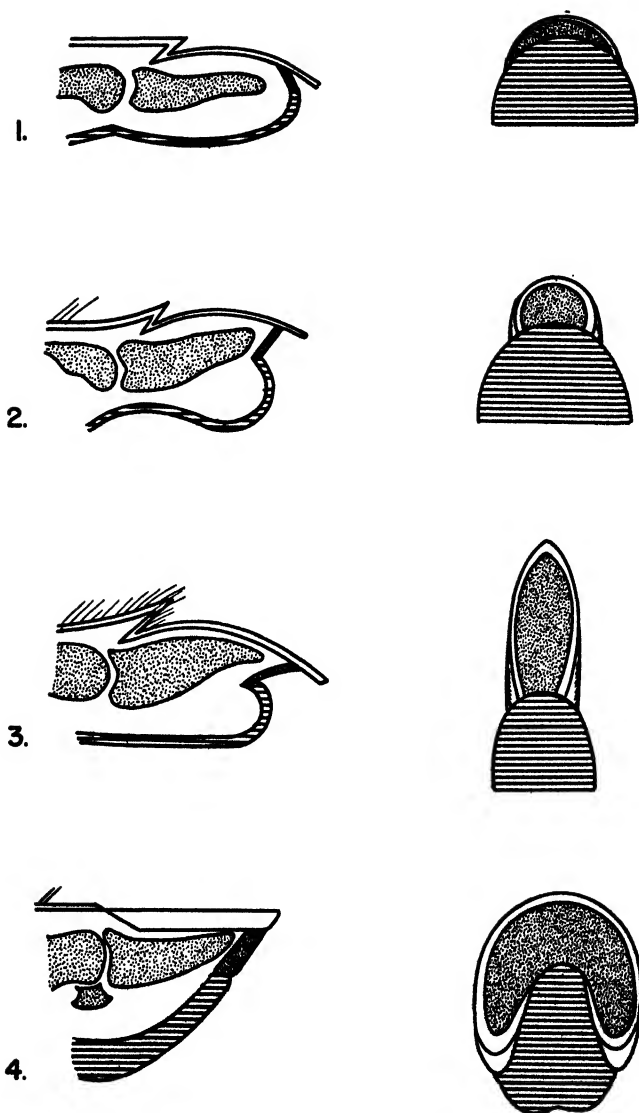


FIG. 62. Claws, hoof, and nails. 1, nail; 2, claw; 3 and 4, hoofs. The unguis is clear, subunguis stippled, ball of digit ruled. (Courtesy The Blakiston Company.)

nail with the finger pad. Its position makes possible the high development of the digital tips as tactile organs. Growth occurs at the base of the nail from the clear stratum lucidum of the epidermis.

Horns. Horns are confined largely to mammals and are of two types. The first, of epidermal origin, may be a solid, keratinized corneal structure such as the horn on the snout of rhinoceros, or it may consist of a cornified or keratinized epidermal portion and underlying core of bone

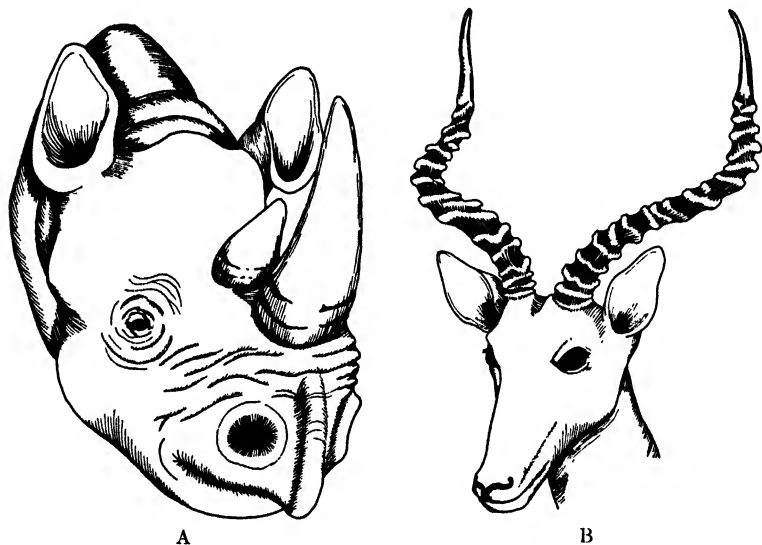


FIG. 63A. The horn on the snout of the rhinoceros is of keratin, akin in structure to the shaft of the hair, and produced by the corneal skin layer.

FIG. 63B. The horn of the African gazelles and antelopes is a permanent horny sheath incasing a bony case at its base.

(Fig. 63A and B). This core, an outgrowth of the frontal bone, occurs as a short knob in cattle.

The second type, of endoskeletal origin, is solid bone. Antlers of elk, deer, and moose belong to this class. These horns when "in velvet" have a skin covering which gives nourishment to the growing tines. This covering is sloughed when growth is completed. Endoskeletal horns, usually confined to males, are shed seasonally, in contrast to the permanent hollow horns of cattle which are present in both sexes and which are not shed. In the American pronghorn (*Antilocapra americana*), the horns are mounted on bony knobs, as in cattle, but only the

outer sheath is shed, while the bony core is permanent. The giraffe shows another curious modification of the horns. In addition to the permanent, prominent bony knob of the frontal bone, two smaller pairs lie on the dorsum of the head.

¹ *Hair.* Hair, a distinctive characteristic of mammals, takes a variety of forms, colors, and also functions. It is most commonly a body covering; in addition, specializations like vibrissae, constituting the "whiskers" of many carnivores, have tactile functions. In nose and ears they protect against dust and invasion by insects. The neck fur of carnivores is particularly heavy, guarding this vital area. In the white-tailed deer, white color over the buttocks apparently serves as a signal. In man, the body hair is greatly reduced, but this loss is even greater in aquatic mammals like walrus, whale, and manatee, whose hair is almost completely gone. Apparently, in man, growth and maintenance of body hair are under one set of hormonal controls, while those of head hair are under another. In man, too, facial hair is an adornment in the male and unwanted in the female, while head hair in the female forms one of her allures and thus is the basis for an industry giving employment to thousands. In absence of his own body hair, man's ingenuity has enabled him to use the hair of other animals in his clothing.

Hair originates from the epidermis. Epithelial columns push downward into the corium from the germinative layer at the sites of the future hair. Eventually the termini of these columns expand and become *hair bulbs*. A *dermal papilla* furnished by the corium pushes into the center of the bulb from below. The epidermal cells at the margins of the bulb proliferate and cause the upward growth of the shaft. With eruption of the hair through the pit at the mouth of the hair follicle, we distinguish a root extending from bulb to epidermis and a shaft or body of the hair, beyond the surface. In large hairs the root may be covered by a thin connective sheath of the corium, to which are attached smooth muscle fibers, the *arrectores pilorum*, which govern movement of the hair. The shaft is covered by a thin, scale-like *cuticle*. The *cortex*, under the cuticle, consists of cornified cells forming a dense, somewhat elastic layer. The center of the shaft, the *medulla*, is made up of degenerating cuboidal cells, largely converted to keratohyalin, together with vacuoles, or air spaces, resulting from the changes in the cells. Many hairs lack a medulla.

Sebaceous glands open into the hair follicle (Fig. 64). Their secretions keep the keratinized hair soft and act as water repellents. Hair or fur color is due to the pigment in the cortex. Waviness of hair is produced by variations in the thickness of the cortex. A straight hair has a cen-

trally placed medulla; waviness or kinkiness appears when the medulla is acentrally placed.

Mammalian skin glands. Glands of cyclostomes, fishes, amphibians, reptiles, and birds have already been considered. The glands of mammalian skin are of three types, sebaceous, sweat, and mammary.

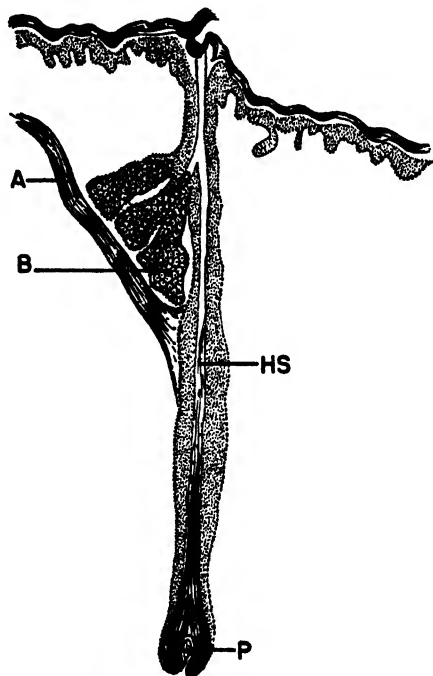


FIG. 64. Section through human scalp. A, root of hair with erectile muscles; B, sebaceous gland; HS, hair shaft; P, papilla. (Modified from Maximow and Bloom, after Schaffer.)

Sebaceous glands. Sebaceous glands, scattered over the skin of the body, provide an oily secretion which protects the body against excessive drying and, as indicated, is water repellent. They are of the alveolar type, with grape-like clusters of secreting cells arranged as small outpocketings opening into a common duct usually associated with a hair follicle. They are derived from the stratum germinativum, which pushes deeply into the corium at the site of the gland, and their secretion is brought about by a transformation of the cell substance

into oil, with consequent destruction of the cell. Such glands, in which the cell is destroyed to furnish the secretion, are termed *holocrine glands*. Modifications of these glands in the orbital region of the antelope produce a specialized musk secretion. The *anal glands* of many Carnivora serve a protective or sexual function. They reach the peak of obnoxious development in the skunk. *Prescrotal glands* of the civets and *preputial glands* of the muskrat belong in this category. The *meibomian glands* of the eyelids are further sebaceous modifications. In mankind, special sebaceous glands are also found in the glans penis, the prepuce, and the labia minora. The *lacrimal gland*, a specialized cell aggregate, carries considerable salt in its serous secretion.

Sweat glands. These are long, spiraled tubes resulting from downward growth of the statum germinativum at specific points in the skin of mammals (Fig. 65). Commonly the secreting portion is coiled. In man they are distributed generally over the body; in many other mammals they are restricted to certain areas, as the tongue of the dog and the ear of the hippopotamus. They are *apocrine* in character, which means that the upper free part of the cell contains the accumulated secretion. This part is pinched off without killing nucleus or cytoplasm; after a recovery period the process is repeated. The characteristic body odors which appear specific for different human races are produced by the sweat secretions.

Mammary glands. Mammary glands crigate from milk ridges, which appear early in mammalian embryonic development (8-mm. human embryo). During this development, thickenings occur along the epidermal ridge, corresponding to the number of nipples and glands to be developed. The milk glands grow from these thickenings by downward proliferation into the corium. The radial arrangement of these cells results in clusters of tubules opening at their distal ends into the excretory ducts of the gland. The cells are not destroyed in the secretion of milk. They are classi-

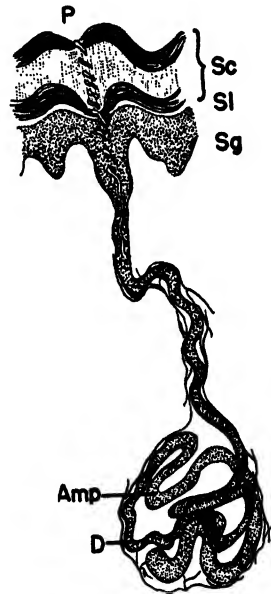


FIG. 65. Human sweat gland. P, pore; Sc, stratum corneum; Sl, stratum lucidum; Sg, stratum granulosum; Amp, ampulla; D, duct. (Redrawn from Maximow and Bloom, modified from V. Brunn.)

fied as apocrine glands and apparently represent a transition from merocrine and holocrine glands. The cells of such glands act simply as agents for the secretion without loss of their vital parts (Figs. 66, 67).

Photophores. Some elasmobranch and teleost fishes, particularly certain denizens of the deep seas, possess light-emitting glands of ectodermal origin known as photophores. These glands are variously distributed over the surface of the body. In certain fishes they are serially

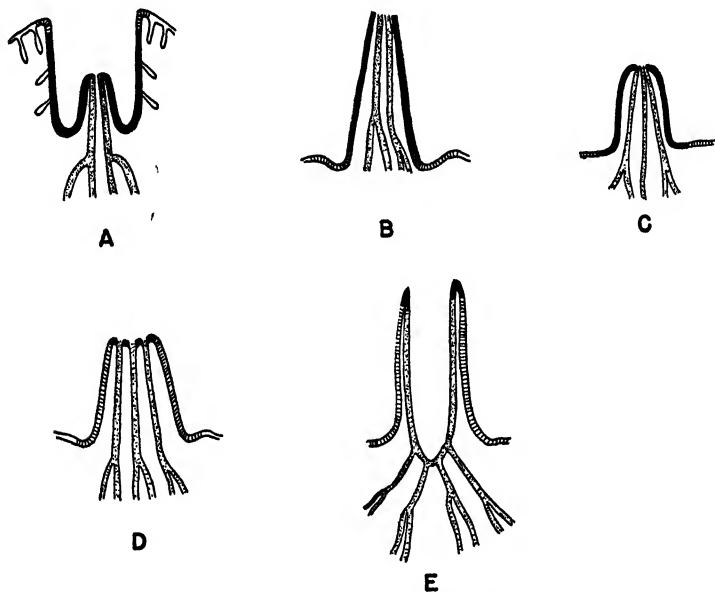


FIG. 66. Nipples in various mammals. A, marsupial in "dry" state; B, in milk-containing state; C, primate; D, carnivore; E, ruminant. Note large milk canal in E, which is fed by milk ducts. In Primates and Carnivora, ducts open directly in the nipple. (Redrawn from Bütschli and Ihle.)

arranged along the sides, resembling miniature, lighted portholes; in others the glands cluster about the eyes or the fins; in the group of the *Pediculati* they are on the terminus of the tentacle-like first ray of the dorsal fin. The glands function, apparently as lures, enticing victims to the vicinity of the lantern bearers; in other instances they are presumed to act as identification symbols whereby males and females of a species recognize each other.

Structurally the photophore in the elasmobranchs is a cluster of

cells of ectodermal derivation, partly surrounded by pigment. These cells have the peculiar ability to secrete luciferin. In some teleosts a lens system is formed of clear cells, or an overlying scale becomes clarified to act as a lens. The posterior wall of the organ in such cases has a pigmented lining serving as a reflector. Together, light-producing cells, lens, and pigment constitute a mechanism akin to a flashlight. Luciferin, secreted by the gland, is oxidized upon stimulation, resulting in the emission of "cold" light.

The integument is a dynamic rather than a static system. It is not a mere shell, separating the animal from the outside environment,

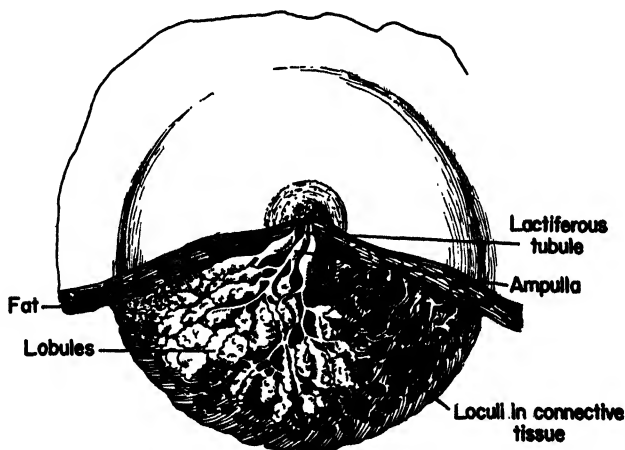


FIG. 67. The human breast during the lactation period. (Redrawn from Luschka and Gray.)

but a complex membrane, informing it of the outside world and adapting the organism to variations in temperature from without and within. The integument of the elephant and the mouse play different roles, although the skin has the same basic layers in both. The great size of the elephant requires constant heat dissipation, which takes place largely through the skin; the diminutive size of the mouse, on the other hand, demands constant heat conservation. Capillary beds which may be collapsed or expanded, depending upon the needs of the animal, are active in such temperature regulation. Ultraviolet light plays a part in supplying the body with the vitally essential vitamin D, or antirachitic agent. Recent tests of the thick hide of the alligator indicate that some ultraviolet absorption takes place through this source.

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CHAPTER 4

THE SKELETON

ROLE

The skeleton, an integral and supporting part of the plant or animal body, appears at both unicellular and multicellular levels. While some organisms exist without specialized supports, the higher ones have skeletal features built prominently into their anatomy.

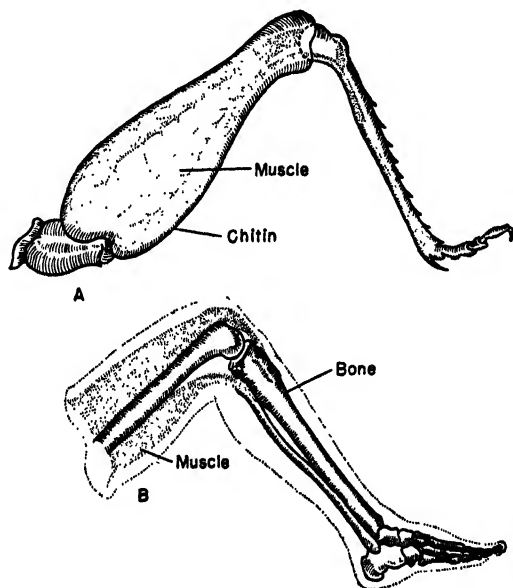
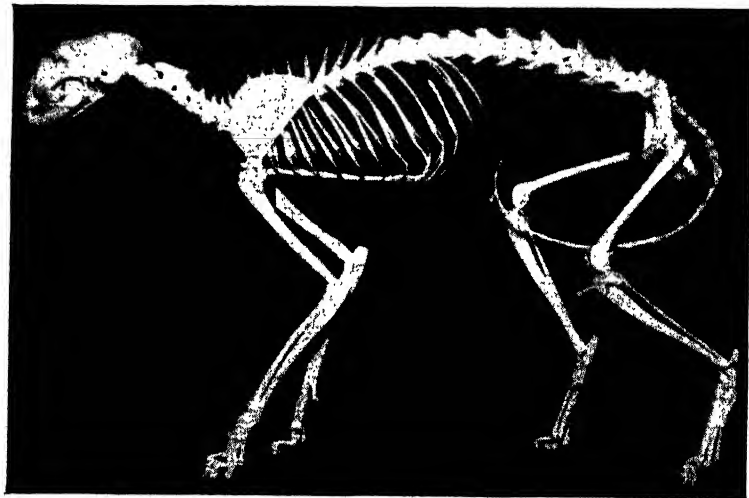


FIG. 68. A comparison of exoskeleton and endoskeleton. A, The third leg of the grasshopper, in which the chitinous exoskeleton covers the muscle. B, the human leg; muscle covers the endoskeleton.

We recognize exoskeletal and endoskeletal systems, the former the rule in the invertebrates, the latter in the chordates (Fig. 68). Associated with movement as well as with static support, the skeleton has muscles attached to it. This is not invariably so, for, in the protozoan



A



B

FIG. 69. *A*, the backbone of the dog. Seven cervical, 13 thoracic, 7 lumbar, 3 fused sacral, and 18 caudal vertebrae constitute the column. *B*, the column is highly differentiated in land mammals.

Radiolaria and Foraminifera, supporting functions antedated the appearance of muscles; the skeleton in such primitive animals is a protective framework for protoplasm.

In lower chordates the skeleton includes primarily the notochord and connective tissue which, in the vertebrates, is largely replaced by the articulating backbone (Fig. 69*A*, *B*). To this are added skull, gill,

and fin supports, with pectoral and pelvic appendages in more advanced chordates. In the Tetrapoda, the land animals with four limbs, the appendages become elaborate lever systems with an increasing number of true articulations, or "breaks," at strategic points.

Supporting structures, in their evolution, have been profoundly modified and subjected to adaptive mutational changes, just as were the other bodily systems. Again it is convenient to use the term *adaptation*, for in its transformation the skeleton has, along with the rest of the body, adapted the animal to various media—land, water, air, and subterranean activity. It has played a part in fashioning the hunting carnivore, the aquatic seal, the flying bird, and the digging mole. In its rise, visceral arches were redesigned for new and strange uses. Jaws, ear ossicles, laryngeal supports, to mention but a few adaptations, are results of this modification. Ribs appeared, first as protective supports, later forming, with associated muscles, the respiratory bellows. The labile nature of the body framework is shown in any of its divisions whether we consider the skull, jaws, ribs, backbone, or appendages. Mutation, entirely through chance; orthogenesis, in the sense of directed development; and apparently even use and disuse have had a hand in its shaping. It must be remembered that the last two indicated phenomena are the apparent effects of more profound and fundamental mutational processes.

Today we look on the contemporary fauna about us as temporary end points in an evolutionary ascent in the sense that they mark the present status of animal lines. These lines, however, are not static, and if we could see the end points 50,000 or, better, 50 million years hence, we should undoubtedly find many skeletal changes that at present we could not hope to predict. The temporary halting points of this heterogeneous animal growth mark the various levels of being which determine the niches to be occupied, the part to be played, the functions to be exercised by every contemporary actor in the animal or human world.

THE NATURE OF THE SKELETON

Supporting tissues, including connective tissue, ligaments, tendons, cartilage, and bone, are derived from mesoderm. In contrast to most other tissues, cellular secretions rather than cell bodies or their processes constitute the bulk of the actual supporting structures. The cells, of mesodermal origin, are the formative agents abstracting from the blood the necessary elements of which skeletal tissues are built.

Connective Tissue. Connective tissue becomes differentiated early in embryonic life (Fig. 70A, B, C). Mesenchymal cells are scattered

between the ectoderm and the developing endodermal tissues. Through coalescence and intermingling of their fibers, a network is built and differentiated, subsequently, into collagenous, fibrous, perichondrial, periosteal, tendinous, and membranous connective tissue. It may acquire special properties, as in elastic tissues, where this quality is desirable; adipose, for deposition of fat; reticular, associated with lymph glands, liver, and spleen. It is a ubiquitous substance, its albuminoid collagenous matrix yielding a gelatinous glue on boiling; it may be inelastic or elastic, giving support to other structures, forming tendons, ligaments, or membranes. As a reticulum it supports liver cells, lymph-

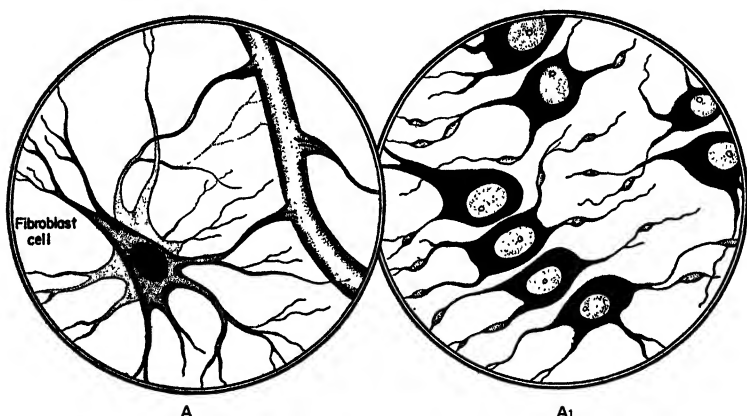


FIG. 70A. Fibroblast cells give rise to connective tissue. Their processes extend as collagenous fibers.

oid cells in the spleen, blood-forming cells in bone marrow, and renal tubules in the kidneys. It may not be dismissed lightly, and its functions, particularly those of the reticuloendothelial tissues, are far from completely explored.

Periosteum, a dense connective tissue surrounding bone, is a collagenous fibrous membrane giving rise to fibroblast cells, which in turn develop into osteoblasts, the latter responsible for bone formation. This type of bone growth from a specialized membrane is designated as *intramembranous*, in contrast to that formed inside cartilaginous structures, when it is known as *enchondral* bone growth.

Cartilage. Cartilage, like bone, arises from connective tissue. Pre-cartilaginous tissue is first formed by accumulation of connective tissue in the areas of future cartilaginous growth. Proliferation of an inter-



FIG. 70B. Collagen fibers at 30,000 magnification. (*Courtesy of the Stamford Research Laboratories, American Cyanid Company.*)

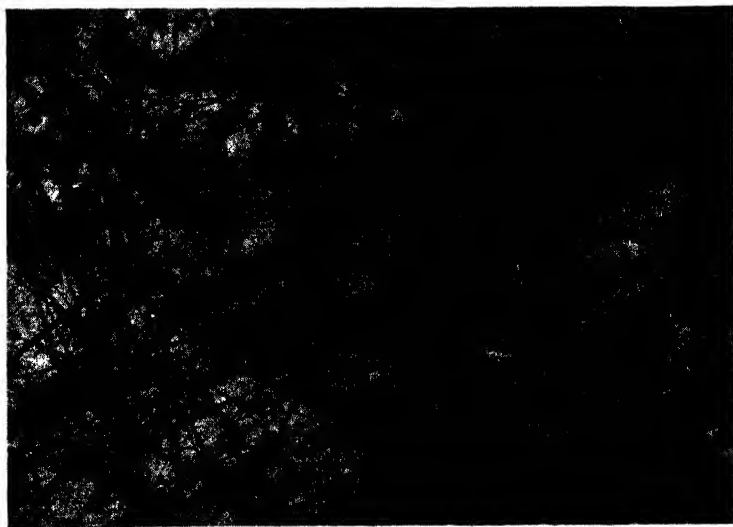


FIG. 70C. Areolar connective tissue. (*Courtesy of the General Biological Supply Company.*)

stitial matrix separates the precartilage cells. By secretion of fluid in the cells and accumulation of the cartilage "precipitate" outside the cell bodies, the fibrillar character is gradually concealed, except in some specialized types of fibrous cartilage. A covering perichondrium is responsible for deposition of the cartilage at the surface of the formation. Such secretions by the perichondrium are characterized as appositional growth.

Cartilage yields chondrin on boiling, a substance similar to the collagen extracted from ordinary connective tissues. The characteristic

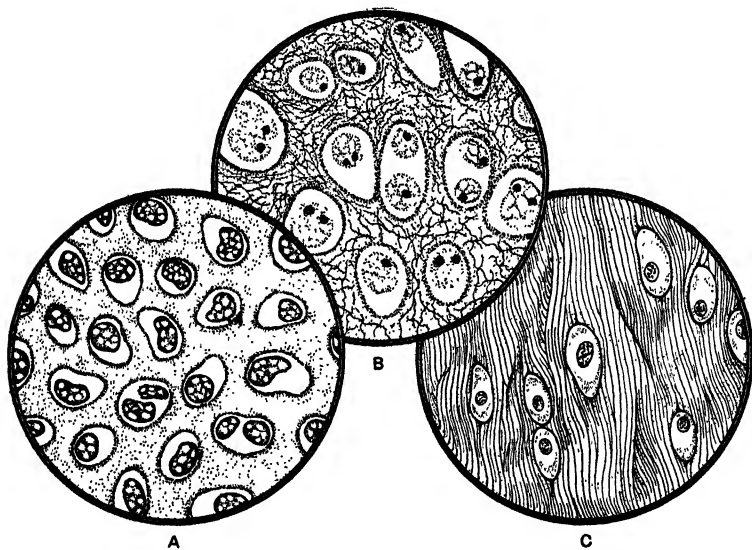


FIG. 71. *Types of cartilage.* A, hyaline; B, elastic; C, fibrocartilage

histological appearance of cartilage is due to imprisonment of the cells responsible for its deposition and their subsequent division within the matrix. This brings about small, encapsulated islands of one or, more frequently, of several cells surrounded by cartilage. With loss of plasticity of the matrix and its accretion, the whole mass assumes a homogeneous milky appearance.

The several types of cartilage recognizable in the body include *hyaline cartilage*, *elastic cartilage*, and *fibrocartilage* (Fig. 71). Hyaline cartilage, the most widespread, occurs on the articulating ends of bones, in the walls of the trachea and bronchi, and in the costal cartilages. It is

bluish white, semielastic, and covered by the tough, fibrous perichondrium. Elastic cartilage, yellow, and characterized by intermingling fibers in its substance, supports the outer ear, the epiglottis, and other isolated parts. Fibrous cartilage, as the name indicates, contains dense connective-tissue bundles and represents a transition between connective tissue and hyaline cartilage. It occurs in certain slightly movable articulations, in the menisci of the knee, the wrist, the sternoclavicular joints, etc. Ligaments are largely white fibrous-tissue bundles. Generally inelastic, they are extensible in the ligamentum nuchae, the head-supporting ligament in the neck, and the ligamenta flava, which unite the lamina of the vertebrae.

Bone. Bone, the hardest and most permanent body tissue, retains despite this quality a certain degree of elasticity. Derived, as indicated, from connective tissue, bone represents its most highly differentiated state. Its hardness stems from its calcium content. Human bone contains about 30 per cent of organic substance and water and 70 per cent of inorganic substance. The inorganic substance includes 58 per cent of calcium phosphate, 7 per cent of calcium carbonate, 1 to 2 per cent each of calcium fluoride and magnesium phosphate, and less than 1 per cent of sodium chloride.

Histology. On examining a section of bone we recognize a *spongy*, or cancellous, part inside a more *compact*, ivory-like outside layer (Fig. 72A and B). In long bones, for example, the wall of the shaft is compact bone, its lumen is partly compartmented by cancellous bone, and at the ends the compact is but a thin covering for the spongy bone underneath. The spongy tissue is arranged in lines more or less parallel to the chief lines of stress. In flat and irregular bones the compact covers both outer surfaces and encloses the spongy layer between. Compact bone is covered with periosteum, a connective tissue whose inner surface contains bone-building osteoblast cells. The periosteum, which also serves as an attachment for tendons, is traversed by periosteal vessels on their way to the marrow cavity within the bone. These vessels enter the cavity by small pores, the nutrient foramina. At the bone ends, periosteum is replaced by articular cartilages.

The bone cavities contain either yellow or red marrow, the former mostly in the shafts of long bones, and largely fat. The red marrow, in the vertebrae, in the ends of long bones, and in flat and irregular bones, is the seat of blood-cell formation. The marrow cavity of the sternal plate, for example, is an important source of blood-cell generation. Both red corpuscles and white granular blood cells are formed in the red marrow. Characteristic osteoclast cells, responsible for tearing down

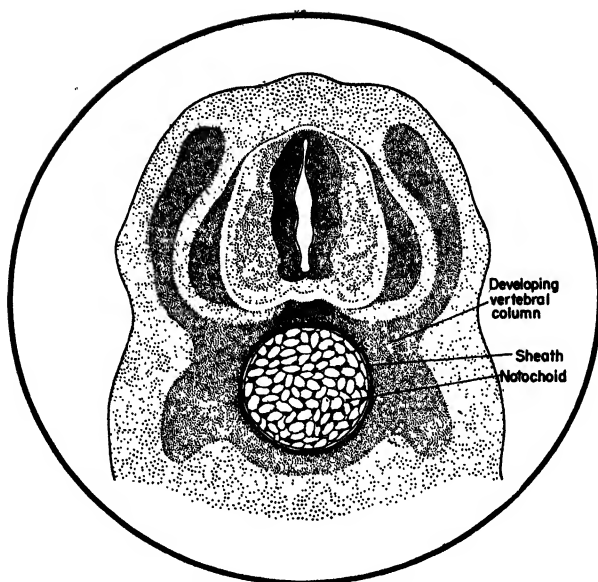


FIG. 72A. Developing vertebral column in the bird. Observe the notochord and the surrounding mesenchyme.

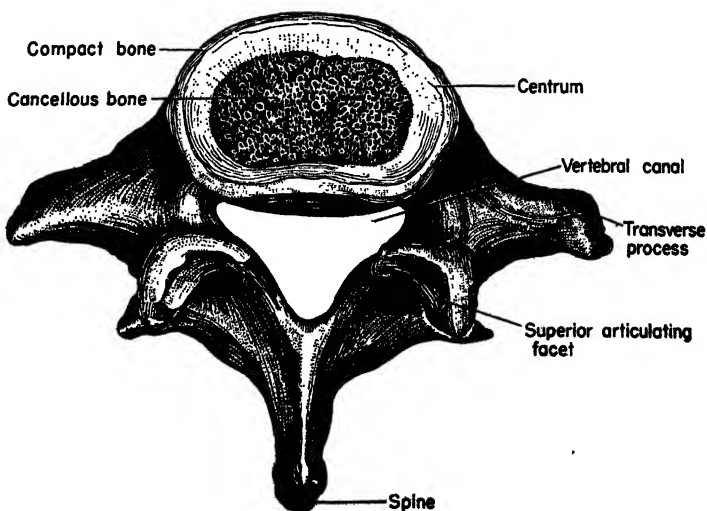


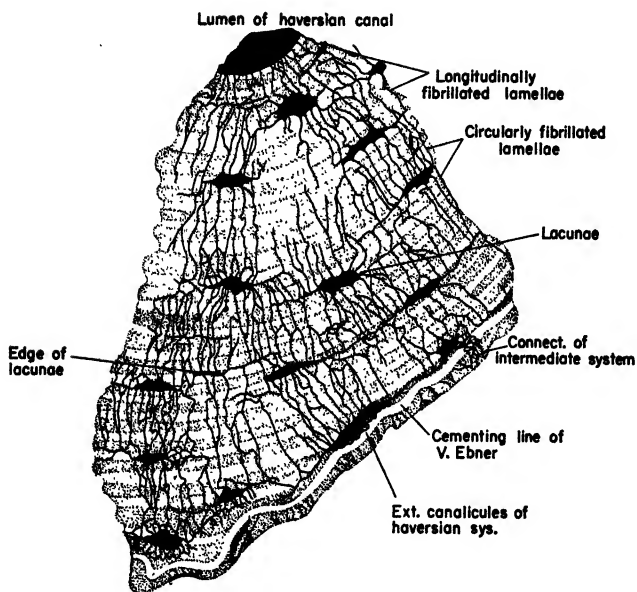
FIG. 72B. A typical mammalian thoracic vertebra. Note in the centrum the compact outer and the cancellous inner layers.

and excavating bone, also are plentiful. Apparently, activity of the osteoblasts, or bone-building cells, and osteoclasts, or bone-destroying cells, is regulated by the parathyroid gland. In hyperparathyroidism, which involves extensive bone pathology, abnormal thinning in certain areas and accumulations of bony tissues in others may be associated with an increase in both osteoblast and osteoclast cells.

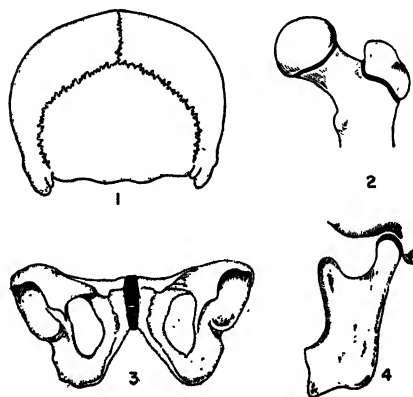
Bone cells are sharply differentiated from their interstitial substance, which is largely infiltrated with calcium salts (Fig. 73A). Compact bone differs in structural detail from cancellous, or spongy, bone. Its histology is best studied in specially prepared cross sections, made by grinding the section to extreme thinness or by decalcification and sectioning. In ground sections, microscopic examination reveals a series of concentric, bony rings perforated by sizable openings in their centers. Such a concentric series of rings is a *haversian system*, the central opening the *haversian canal*, and the bony rings the *lamellae*, or bone plates. This arrangement arises from the addition of new lamellae at the outside of those already formed during development of the bone. Lamellae vary from 3 to 9 microns in thickness. Between the lamellae are minute bone cavities, the *lacunae*, which in life are occupied by the *bone cells*. Thin lines radiate from the lacunae. These are the *bone canaliculi*, which anastomose with each other and connect various lacunae in a haversian system. At the margin of a system the canaliculi loop back into the lamellae and reenter their lacunae. Small blood vessels and lymphatics traverse the haversian canals throughout the compact bone. They are the nutrient agents for the bone and marrow. At the outer and inner surface of the bone the canals open by minute pores that offer ingress and egress to the vessels. The interspaces between complete haversian systems are occupied by *interstitial lamellae* of irregular pattern, while at the bone surface are *basic lamellae*, running parallel with the long axis of the bone.

Covering these basic lamellae is the periosteum, generally closely adherent to the bone. After growth is completed, osteoblast and osteoclast cells disappear from the periosteum. Injury, pathologic disturbances, or bony transplants may evoke a reappearance of these cells. The endosteum, a thin connective tissue, lines the marrow cavities. It has bone-building and bone-destroying properties similar to the periosteum. In the rebuilding of bone during growth or in healing, these tissues are of vital importance, since in their absence bone growth does not take place.

Cancellous bone, which precedes the compact and from which the latter is derived, is more irregular than the compact type. Its com-



A



B

FIG. 73. *A*, sector of a cross section of an haversian system of a macerated human hipbone. The cavities and canaliculi are filled with a dye. (*Redrawn from Maximow and Bloom.*) *B*, types of articulations. 1, synarthrosis; 2, syncondrosis; 3, amphiarthrosis; 4, diarthrosis.

ponents are adapted to the particular strains to which they are subjected.

Bone may arise directly from osteoblast cells formed in specialized connective tissue instead of first passing through a cartilage stage. When so formed it is called *membranous bone*, and, as indicated, the process is called intramembranous ossification. Collections of collagenous fibers give rise to irregular patches of osteogenic substance, gradually uniting into definitive bone. Bones of the jaws and the calvarium are of this type.

More frequently, bone first passes through a hyaline-cartilage stage. This transformation, as noted, is *enchondral ossification*, and bone so formed is termed *cartilage bone*. It involves destruction of the cartilage and substitution of bone through specialized connective tissue. There is no discernible difference between membrane and cartilage bones once they are formed.

Hobart M. Smith has recently suggested a classification of bone which distinguishes clearly between ontogenetic and phylogenetic types.

As ontogenetic types he recognizes cartilage, membrane, and chondromembranal bones. The first is preformed in cartilage, the second directly transformed from mesenchyme, or connective tissue, and the third type formed partly of cartilage bone tissue and partly of membrane bone tissue.

As phylogenetic types he distinguishes between primary and secondary bones. Primary, the oldest phylogenetically, are homologous with or derived from the endoskeletal elements of the Chondrichthyes. This type of bone passes through a cartilaginous stage. The secondary bones are added to the primary and are independently derived from the deep layer of skin (derma) or from subcutaneous (subdermal) tissue independently of the skin. Certain fused bones which may involve both primary and secondary elements, he classifies as compound bones. The heterogenous phylogeny of a bone is thus expressed by the designation *compound* while heterogenous ontogeny is described by the term *chondromembranal*.

Joints. The skeleton of the vertebrate animal is a jointed mechanism. Certain joints, like the sutures of the skull, are immovable (Fig. 73B). In spite of this immobility, thin cartilages separate the bones until fusion takes place with the completion of growth. Such articulations are *synarthroses*. Segments of the vertebral column are so united by the intervertebral discs that slight movement is possible where disc surfaces meet. These articulations are *amphiarthroses*. In animals with bony skeletons the shafts of long bones (diaphyses) become fused

with their heads (epiphyses) at different age levels, depending upon the species and the particular bone. Prior to fusion, the heads and shafts of long bones, just as the bodies of contiguous skull bones, are separated by thin lines of hyaline cartilage. Such temporary joints are *synchondroses* and represent a special type of synarthrosis. This variability in suture closing is used in assessing the skeletal age, particularly that of the human being, since the time of closing is quite specific for a given joint (Table 2).

TABLE 2. AGES OF SUTURE FUSION

Sternum	Between puberty and age 25
Sphenoccipital joint.	Before age 25
Frontoparietal joint.	Age 26
Femur	Proximal end, 18th year; distal end, 20th year
Tibia	Proximal end, 20th year distal end, 18th year
Innominate (pubis, ischium, ilium)	25th year
Clavicle (1st to ossify)	Unites at 25th year
Parietomastoid	Unites at 27th year
Occipitospheoid	Unites at 25th year

Our knowledge of suture closing is frequently applied in cases of partial destruction of the body. In the great gas-explosion disaster in Cleveland, Ohio, 1944, in which some 328 persons were killed, many bodies were so badly burned and charred that age and sex had to be determined by skeletal findings. X-ray pictures, in this instance, of the pelves and other bones and articulations enabled those assigned to this problem to establish sex and age identities in most cases. In animals other than man, bone growth, too, follows a regular pattern, and sutures close in definite sequence. Effects of experimental interference in delaying or advancing the time of closing are valuable criteria for assessing the effectiveness of the interference. The late T. Wingate Todd made important contributions concerning the retarding effects of childhood diseases upon bone growth through his studies on skeletal growth. He was able by X-ray studies of the skeleton to establish the approximate time and duration of certain diseases causing skeletal retardation and to determine the difference between skeletal and chronological age after such diseases.

The third basic type of joints, or *diarthroses*, are the most usual articulations in land vertebrates. Joints in this category permit the greatest degree of movement. They are divided into hinged (ginglymus), ball-and-socket (enarthrosis), and gliding types (arthrodia). Such artic-

ulations are surrounded by joint capsules of tough connective tissue, aided by supporting ligaments, their fibers adapted in strength and direction to the particular stresses to which the part is subjected. The capsule is lined with a synovial membrane that secretes the lubricating synovial fluid in the joints, and the heads of the bones within the capsules have a cartilaginous facing. In some joints, menisci, which are semilunar-shaped cartilages, partly or entirely divide the joint cavity. Such cartilages are held in place by the capsule, which is joined with them at their periphery.

Articulations are important sites for the initiation of sensory (proprioceptive) orienting impulses. These are carried to the cerebellum, particularly in land animals, where constant balancing adjustments are necessary. Automatic adjusting movements are the ever-recurring sequelae to these sensory disturbances.

THE SUPPORTING COLUMN

For descriptive purposes we may divide the skeleton into axial and appendicular parts. Included with the first is the skull, vertebral column, ribs, and those parts of visceral origin known collectively as the branchial skeleton. Included with the appendicular division are pectoral and pelvic girdles and appendages.

The chordate animal is bilaterally symmetrical; most frequently it is elongate, cylindrical, or fusiform. Given this architecture, a supporting beam is necessary. This is the plan we follow in the construction of ships, where the keel becomes the great supporting beam from which the ribs radiate, or in our houses, where the roof-tree is the central support for the rafters, which are tied to it. Our own vertebral beam has the great advantage of flexibility in comparison with keel or roof-tree, and because of our bipedal posture the beam usually stands on end, becoming a boom or a mast.

Among water inhabitants, great flexibility has been retained in this supporting rod. In protochordates it is fibrous or cartilage-like and without articulations. Its elasticity is sufficient to permit side-to-side movements, and together with the segmental musculature it is the great locomotor organ, not only of protochordates, but also of cyclostomes and fishes. In cartilaginous fishes it becomes an articulated column, a true "backbone," even though it remains cartilaginous. The large number of vertebrae closely joined by ligaments retain flexibility of the column as a whole through the limited movement permitted at their contiguous surfaces. Tough, fibrous intervertebral discs separate the adjacent segments. Such a column is relatively undifferentiated

in the cartilaginous fishes, although size differences between tail and body vertebrae do appear. In the bony fishes, while ossified, it retains the general undifferentiated appearance it has in cartilage fishes.

In dissection we of necessity study isolated systems. It must be remembered that, in the living animal, systems work together. In the case of the supporting column, this means that muscles affecting movement are associated with it, as are also the nervous and circulatory systems. The segmental pattern of the muscles gradually becomes obscured in advancing from *Amphioxus* through the fishes and to the land mammals. Nevertheless, embryological study demonstrates the segmental nature of the muscles associated with the column in all classes. These muscles are responsible for the side-to-side sweep of the piscine body and together with the tail are its true propulsive mechanism.

Other functions are served by the column. To it are attached various mesenteries; these support the liver, intestine, internal reproductive organs, etc. In the gill region, the gill, or branchial, bars are connected by ligaments to the vertebral column. Ventrally they are united through copulas. By these dorsal and ventral attachments the arches may be moved forward or back, in opening or closing the gill clefts. Further structures attached to the fish column are the pectoral and pelvic girdles, the foundations for paired fins and land appendages. The pectoral girdle is directly attached by muscles and indirectly by a clavicle in many species. In contrast the pelvis retains a more complete bony articulation with the column through the sacrum. The skull articulates with the column; in fact, the latter is its chief skeletal support. In the chordate series through the reptilian level the long axis of the skull is commonly in line with the column. In amphibians, paired occipital condyles form a definite articulation between skull and column, although the degree of movement is small. In reptiles a single articulating condyle below the foramen magnum unites head and skull. In birds and mammals double condyles occur. Increasing head movement characterizes the evolution of this articulation.

The above-listed functions ascribed to the column are those of support. It has in addition great protective value for the spinal cord, just as does the brain case for the brain. The spinal cord is securely housed in the bony canal formed above the vertebral centra and underneath their dorsal processes, the laminae. The laminae, two in number in each vertebra, except in the caudal, are flat outgrowths joining the centrum by the pedicles and fusing in the middorsal line as the dorsal spines. At their attachments the pedicles are excavated above and

below to form vertebral notches. The lower margin of one notch meets the upper margin of the one below it; together they create a circular neural foramen for the exit of the spinal nerves. Blood vessels also find ingress and egress to the cord through these openings. The spinal canal and the foramina do not extend into the caudal vertebrae. In tetrapoda the spinal cord does not extend the full length of the lower lumbar or sacral column but terminates at the lumbar level. The lower portion of the canal is occupied by the proximal ends of spinal nerves, which emerge through neural foramina at lower levels and unite into the plexuses supplying the pelvic appendages.

It has been pointed out that in the protochordates and fishes the column is largely undifferentiated. Some reduction in size is noted in the fish column at the cephalad and the caudad levels. In tailless amphibians, like the frog, the entire skeleton is highly specialized, correlated with peculiar habits of locomotion. The backbone does not escape this specialization, for the column is reduced to nine vertebrae and a urostyle, the latter uniting the column with the pelvic girdle.

Development and Comparative Anatomy. Considerable controversy has existed concerning the origin of the notochord. Above the protochordate level it undoubtedly is of mesodermal derivation, while in the latter it originates from the endoderm of the gut wall. In *Amphioxus* it is made up of large vacuolated cells, in which semirigidity is gained by internal pressure, or turgor, within the vacuoles. Two layers surround the cellular matrix, the inner a secreted layer, the outer of connective tissue.

In cyclostomes and in primitive ganoid and dipnoan fishes, the notochord is retained with additions of cartilage. Surrounding it, a connective-tissue sheath embraces the spinal cord and terminates dorsally in a median extension in which cartilaginous fin rays may be embedded. Ventrally the connective-tissue sheath enfolds the aorta and the caudal vein and represents the forerunner of the hemal arch.

Two cartilaginous elements appear on either side in each segment in the connective-tissue sheath surrounding the spinal cord. These differentiate into the neural arch. In cyclostomes and fishes a cartilaginous or bony hemal arch forms also in the connective tissue surrounding the vessels underneath the notochord. Intercalary arches with their apices pointing to the bases of the neural arches complete the protection for the spinal cord. Since the notochord persists in cyclostomes and the dipnoan fishes and in *Acipenser*, and a true centrum is lacking, it is designated as an acentrous column.

At the elasmobranch level true centra are established. These sur-

round and invade the notochord and reduce it to remnants between adjacent vertebrae. In a midsagittal view through the elasmobranch column, each centrum appears as a dorsal and a ventral cartilaginous triangle with the apices meeting or approximating each other at the center of the vanishing notochord. The latter is confined to the regions not occupied by the centra. Each articular surface of the centrum is biconcave; such vertebrae are designated as amphicelous.

The sclerotomes which give rise to the centra are segmental. Sclerotomes, it will be recalled, appear in the mesodermal layer after it has become differentiated embryonically into a dorsal epimere, a lateral or middle mesomere, and a ventral hypomere. The *sclerotome* develops from the *epimere* along with the *dermatome* and *myotome*. The first is responsible for the proliferation of skeletal tissue, the dermatome for the mesodermal layer of the skin, and the myotome for the musculature.

The sclerotome partly surrounds the notochord and the neural tube. Its scleroblastic tissue forms the vertebrae. Temporary vertical divisions appear but do not coincide with the limits of the future vertebrae. The original sclerotomic segments split again, and each posterior half joins the anterior half of the segment posterior to it. This gives an advantage to the muscle fibers originally associated with the segment, since by the splitting of the segments each myotome becomes joined to two vertebrae.

The term *arcualia* designates the cartilaginous elements of the neural, hemal, and intercalary arches. Four arcualia are associated with each segment; the anterior dorsal and ventral pair are the *basidorsal* and *basiventral*; the posterior pair, the *interdorsal* and *interventral*. From the first two are built the neural and hemal arches, respectively; from the last two, the dorsal and ventral intercalary arches.

Centra appear directly in the sheath about the chord in many of the fishes, including the elasmobranchs. This is known as *chordal formation*. Or they may arise from the medial sides of the sclerotome segments and from sclerotome tissue, which proliferates about the cord, designated as *perichordal formation*. In the second type, typical of the Tetrapoda, direct ossification from the membranous stage may occur.

True articulations are absent in the elasmobranch column. The vertebrae are closely joined by ligaments; such fixed articulations are synarthroses. Where freedom of movement is provided at the intervertebral articulations, amphiarthroses result.

Conspicuous in the sharks is a high degree of calcification in the cartilage of the skeleton. This must not be confused with ossification. In calcification, the cartilage is penetrated by calcium salt secretions,

while, in ossification, destruction of cartilage goes hand in hand with deposition of bone tissue.

Articulating condyles joining skull and column are absent save in a few genera (*Rajidae*), rays, sawfish (*Pristidae*), and *Pristiophoridae*. Elongation of skull and special functions of snout, as a directing aid in swimming, appear correlated with these paired condyles.

In the fishes the vertebrae are either cartilaginous or bony, depending upon the group from which the selection is made. The *Chondrichthyes* are entirely cartilaginous, while in the *Osteichthyes* there is a transition from a partly cartilaginous to a completely bony skeleton, which also involves the vertebral column (Fig. 74).



FIG. 74. The skeleton of the fish centers about the vertebral column and the skull. (Photograph by John Warfel.)

The amphibians range structurally from elongate, apodal, snake-like *Gymnophiona* through the fish-like urodeles to the highly specialized saltatorial *Anura*. The backbone does not escape modifications in this heterogeneous class (Fig. 75). The columns are differentiated into cervical, trunk, sacral, and caudal elements. A single cervical, a single sacral, with a varying number of trunk and caudal vertebrae is the rule. Well-defined articulating facets (*zygapophyses*), constituting true arthrodial joints, occur. These movable arthrodiae must not be confused with the amphiarthrodial joints at the centra. The vertebrae are procelous, although in some anurans they may be opisthocelous. In the frogs and toads the column is greatly shortened, an adaptation to their jumping habits. One cervical, seven trunk, and a single sacral vertebra are followed by the urostyle, the latter representing

some 10 fused caudal segments. The single sacral vertebra with the urostyle and the elongate pelvis constitute the pelvic girdle.

In the Apoda, or limbless and worm-like amphibians, the individual vertebrae are long, without spinous processes, and without a specialized sacral vertebra. In the urodeles the total number of vertebral elements

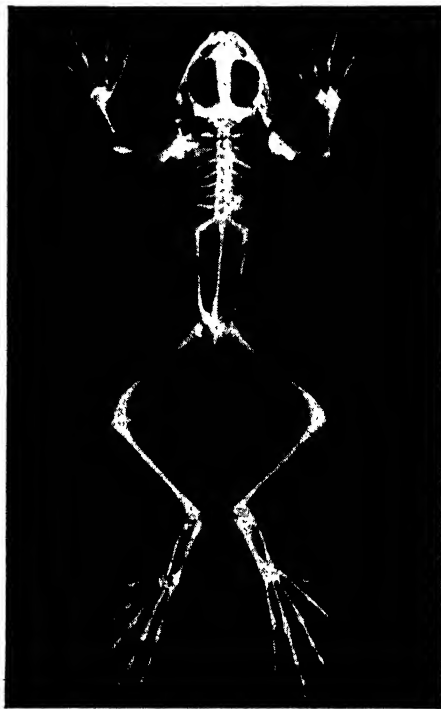


FIG. 75. Skeleton of the frog. This represents a highly specialized skeleton. Note the prominence of the appendicular skeleton in comparison with that of the fish in Fig. 74. (Photograph by John Warfel.)

varies from 12 to 20 in the trunk and up to 30 in the tail. In *Amphiuma* there may be a total of 100 vertebrae.

In primitive reptiles amphicelous vertebral articulations were the rule; in the modern, a procelous type is general. In the lizards the amphicelous condition persists.

The reptilian column, while differentiated into cervical, thoracic, lumbar, sacral, and caudal vertebrae, still retains some primitive char-

acters, particularly in the caudal region, and to some extent in the cervical, through retention of cervical and caudal ribs (Fig. 76). Aside from this, remnants of the notochord persist throughout the column in the lizards, a condition reminiscent of that in the fishes. In the crocodiles these notochordal elements have disappeared almost entirely. In reptiles without appendages no sacral specialization occurs, while in the others two sacral elements have developed. In the turtles a highly specialized skeleton has evolved. Except for the cervical and the

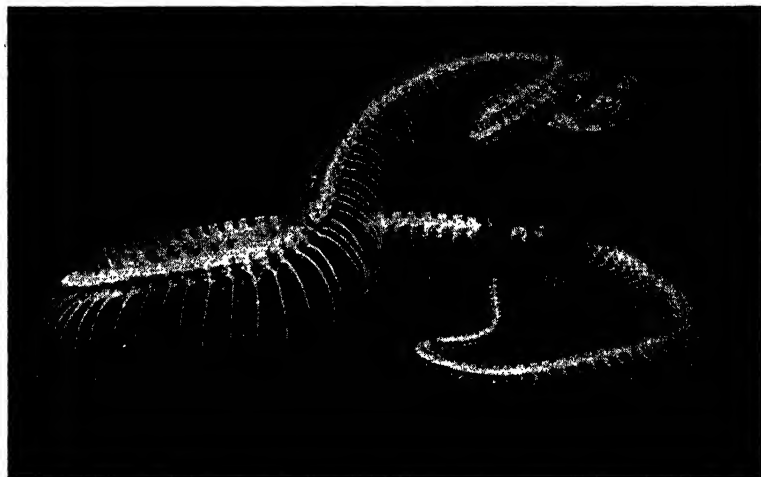


FIG. 76. The snake skeleton. Note the relatively unspecialized state of the column and the presence of ribs associated with each vertebra almost to the terminus of the tail. (Photograph by John Warfel.)

caudal vertebrae, the entire column is fused with the carapace through the neural arches, a fusion which includes the thoracic and lumbar ribs. In the Crocodilia and in *Sphenodon*, with abdominal ribs, the two or three presacral vertebrae which do not have abdominal ribs associated with them are designated as lumbar vertebrae. As many as 9 cervical ribs occur in living reptiles. *Sphenodon*, alligator, and turtle have 8; some of the extinct pleiosaurs, on the other hand, possessed over 40. Trunk vertebrae, including 2 lumbar, number 17 in *Sphenodon*; in the alligator there are 12 to 15 trunk, including 2 to 5 lumbar; in the turtle there are 10 trunk and 2 sacral vertebrae. Caudal elements number 36 in *Sphenodon* and in the alligator, 12 to 18 in the turtle. Two sacral vertebrae are general in these three groups.

As indicated, remnants of the notochord disappear largely in the Crocodilia. Intervertebral cartilages comparable in many respects to those of the mammals separate the centra, although they are relatively smaller, more fibrous, and without the elasticity and the fluid content of the mammalian discs.

Spinous and transverse processes are well developed in the trunk, lumbar, and caudal vertebrae. Arthrodial joints appear at the pre- and postzygapophyses. An odontoid process, the original centrum, belonging to the atlas, has become joined with the axis. This fusion, however, is not complete, since a thin line of hyaline cartilage separates axis and odontoid process throughout life. A single occipital condyle articulates with the first cervical vertebra.

In turtles, ribs are absent in the neck but are retained partially in the caudal region. In the trunk they are greatly expanded and fused with the carapace. The caudal vertebrae also have hemal and neural arches associated with them.

The column of the snake contains the largest number of segments or vertebrae of any living group. There have been counted 435 in the python (*Python molurus*), 192 in Typhlops, against 165 in some of the snake-like lizards (*Ophisaurus*) and 32 in the turtle (*Chelonia*).

The ribs are relatively free in the absence of a sternum in the snakes and together with the column and musculature form a locomotor leverage system by which they move in seemingly effortless fashion. Caudal and precaudal vertebrae are differentiated, with the first two vertebrae modified into atlas and axis.

In birds the number of vertebrae varies from 39 in some of the song-birds to 63 in the swans (Fig. 77). The parts include a centrum, neural arch, spinous and transverse processes, and pre- and postzygapophyses. A ridge or ridges, the hypapophyses, extend ventrally along the vertebrae. Saddle-like opisthocoelous, amphicoelous, or procoelous articulations are found.

Cervical vertebrae vary from 11 to 25, the latter in the swan, the last 2 or 3 usually with attached free ribs. All vertebrae whose attached ribs extend to the sternum are designated as thoracic; these vary from 3 to 10 in number. Their movements are restricted by ligaments; in the flying birds, rib movement is less restricted than in nonfliers like the penguins. Thoracic spinous processes are usually prominent.

A peculiarity of the bird column is the synsacrum of 10 to 22 fused vertebral elements forming a wide support between the acetabula. Associated with these supports are the peculiar ilium, ischium, and pubis, variously fused with the synsacrum. The entire mechanism has de-

veloped in connection with bipedal locomotion and is associated with the forward displacement of the center of gravity. In many respects the specialization of the bird column is analogous with that of the amphibian Anura, where peculiar locomotor habits are correlated with a specialized skeletal axis.



FIG. 77.

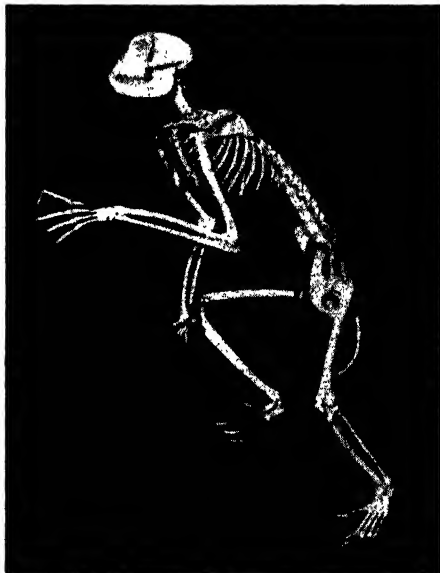


FIG. 78.

FIG. 77. The skeleton of the bird. Some 14 cervical vertebrae characterize the column. Synsacrum, keel, and furcula are other distinctive features. (*Photograph by John Warfel.*)

FIG. 78. Skeleton of the monkey. The brachiating primates have long, slender appendages and elongate digits. The tail is prehensile only in the New World monkeys. (*Courtesy of the General Biological Survey House, Chicago.*)

The mammalian column is differentiated into 7 cervical vertebrae (9 to 10 in *Bradypus*, the three-toed sloth, 6 in the manatee); 9 to 24 thoracic vertebrae, dependent upon the number of ribs; usually 2 to 9 lumbar, with more in carnivores than in ungulates (Figs. 78, 79). The lumbar include the presacral trunk vertebrae without ribs; the sacral may number from 1 to 6 elements, associated with the ilium. The caudal vary, depending upon the tail length, *e.g.*, 3 in the Chiroptera, 33 in some primates, 49 in the scaly anteater. The spines and trans-

verse processes continue as the most noticeable external features of the vertebrae; in the large four-footed ungulates these may be of relatively great size associated with the suspension of the head and neck. The lumbar are characterized by broad transverse processes. In all instances the column becomes ossified, although remnants of the notochord

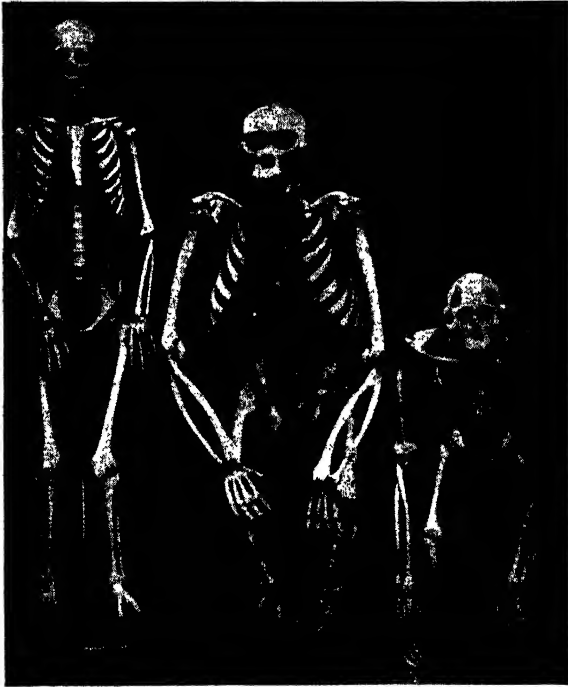


FIG. 79. From the great apes to man there is a progressive lengthening of the hindlimb with concomitant shortening of the forelimb. Man alone of the anthropoids is adapted to a complete upright position. From left to right, man, gorilla, orangutan. (Courtesy of the General Biological Supply House, Chicago.)

persist in the nucleus pulposus of the discs. The neural canal ends in the sacrum.

A Typical Vertebra. A vertebra from the middle thoracic region is most representative of mammalian vertebrae (Fig. 72B). Such a segment has a *body* ventral to a *neural arch*; the latter encloses the vertebral foramen. Together the foramina of the several vertebrae of a spinal column form the *neural canal*, in which is housed the spinal cord.

The vertebral arch joins the body by a pair of *pedicles* at the sides of the foramen. The pedicles are notched at their roots, and when the vertebrae are superimposed, these notches form the *intervertebral foramina*, through which the spinal nerves and vessels emerge.

From the pedicles a pair of *laminae* ascend to complete the arch, and from their junction the *spine* projects posteriorly. Besides the dorsal spine, a *transverse process* extends laterally, one on each side, from the base of the arch.

A *superior* and an *inferior articular process*, the *zygapophyses*, project upward and downward, respectively, on each side. The superior pair, or *prezygapophyses*, have their articular facets directed laterally or dorsally; the inferior, or *postzygapophyses*, ventrally. In an articulated column, the facets on the superior processes face those of the inferior processes of the vertebra above. In life these facets are faced with hyaline cartilage. Facets for the articulation of the heads of ribs (*parapophyses*) occur on the body; those for the articulation of the tubercle of the rib (*diapophyses*) appear near the tips of the transverse processes.

The vertebra is largely cancellous, or spongy, tissue with a covering of compact bone. Numerous small, nutrient foramina open into it for passage of blood vessels.

The body, also called the *centrum*, is cylindrical. To its upper and lower flattened surfaces are attached the *intervertebral discs*. The articulations are amphiarthrodial, permitting a slight amount of movement at each joint. The column is held together by an anterior and a posterior *longitudinal ligament*, the first running along the anterior margin of the body, the second on the floor of the vertebral canal. The intervertebral discs, or fibrocartilages, unite adjacent bodies securely. The arches are joined by a series of short ligaments, the *ligamenta flava*, *interspinal*, *intertransverse*, and *supraspinal* ligaments. The last expands in the neck region to the *ligamentum nuchae*. It is particularly well developed in the large, long-necked ungulates.

Joining the articular processes are articular capsules lined with synovial membranes.

To summarize the functions of a vertebra: It is a skeletal device giving support to the muscles and soft tissues of the body; it permits movement through the amphiarthrodial joints between centra, and the arthrodial joints at the articular processes of the individual vertebrae; it offers, through the laminae and transverse and spinous processes, large surfaces for muscle attachments and, by the neural arch, a safe housing for the spinal cord; it is the fundamental support for pelvic and pectoral girdles and appendages as well as for the head.

Types of Centra. The centra of vertebrae articulate with each other in various ways. The flattened surface of a typical mammalian vertebra has been described. This type is designated as *acelous*, or *amphiplatyan*, since the ends are not hollowed out. In the fishes, it was noted that both ends are concave; typical are the small, cylindrical vertebrae often seen in cooked salmon with their cone-shaped cavities at either end of a segment. This is the *amphicelous* type. In amphibians and reptiles the cephalic ends are concave, while the caudal are convex, resulting in modified ball-and-socket joints. This is the *procelous* type. Another type in birds and in some of the sacral vertebral elements in fishes and reptiles has the convex surface facing anteriorly, the concave on the caudal end forming the *opisthocelous* type.

RIBS

Ribs, absent in the cyclostomes and the holocephalian fishes, first appear in the elasmobranchs as lateral cartilaginous extensions in the horizontal skeletogenous septum. They develop in the myosepta from the same elements responsible for connective-tissue formation. Apparently two types, dorsal and ventral ribs, occur, an observation based upon their appearance at the junction of the vertical and horizontal skeletogenous septa in the elasmobranchs and in the myosepta ventral to these in the dipnoan and teleostome fishes.

In the trunk they surround the body cavity; in the tail they are continued as hemal arches; in the cervical, lumbar, and sacral regions they are commonly vestigial, and their vertebra ends are fused with the transverse processes of the vertebrae.

The ribs of the Tetrapoda are of the dorsal type. The head of the rib articulates with the transverse process by the facets on the centra (parapophyses), while those on the transverse processes (diapophyses) articulate with the tubercles of the ribs.

In Amphibia the ribs were well developed in the extinct Stegocephali (Fig. 25) and in modern urodeles and naked Apoda. In Anura they are greatly reduced and may be fused with the transverse processes. They are not connected with the sternum, although the latter is present. In the Gymnophiona no sternum occurs.

In reptiles, ribs and sternum constitute a basket which gives strong support to the shoulder girdle and the upper ribs. In addition this closed basket with its specialized musculature marks a new method of taking air into the lungs by creation of negative pressure within the thorax, as the result of increasing its volume. In snakes all the ribs are free in the absence of a sternum, and in crocodiles and snakes the

ribs have but a single articulation with the column. This is general in those animals in which the body is not lifted above the ground. In those in which it is elevated some distance above the surface, a head and tuberculum articulate with the vertebrae. Caudal ribs are common in the reptiles. They also frequently possess abdominal ribs, a series of bony supports originating in the connective tissue of the abdominal wall and later acquiring muscle attachments as they



FIG. 80. Gastralia. Abdominal ribs independent of vertebral ribs characterize a number of reptilian species.

sink deeper into the tissues (Fig. 80). *Sphenodon* has 24 pairs of such ribs, while the crocodiles possess 8 pairs. In the turtles, the plastron has an origin similar to that of the abdominal ribs.

The ribs of birds articulate with the vertebrae by the head and the tuberculum; the former is associated with the centrum, the latter with the transverse process. Both vertebral and sternal portions are ossified and join each other at a marked angle. In most birds an uncinat (hooked) process develops on the vertebral part of the rib and overlies the body of the succeeding rib. This device gives additional support

to the costal basket. True ribs joining the sternum vary from three in some of the pigeons to nine in the swan. One to three pairs of free thoracic ribs may be present.

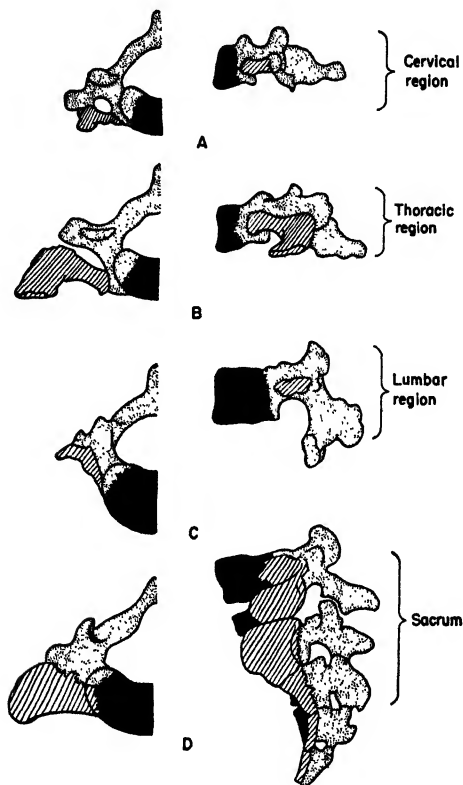


FIG. 81. Cross-sectional and lateral view of rib relationships to vertebral column in man. Ruled segments represent the parts of ribs associated with or fused with the bodies of vertebrae. Note that in cervical, lumbar, and sacral vertebrae these rib elements become a part of the transverse processes. (Redrawn from Cunningham.)

In the human male and female 12 pairs of ribs occur (Fig. 79). They are thin, curved, flat bones attached to the vertebrae by a *head* and *tuberculum*. Anteriorly they join costal cartilages, which in turn articulate with the sternum. The first 7 pairs are true ribs, since their cartilages attach directly to the sternum. The remaining 5 pairs are

false. The first 3 pairs of the false each join the rib above by their cartilages; the last 2 pairs, or floating ribs, are free, since their cartilaginous tips fail to join the costal basket.

Between the head and tuberculum is the *neck*. A short distance beyond the tuberculum each rib makes a sharp forward bend, the *angle*. The shaft is further marked by a *costal groove* along its lower border, in which intercostal artery, vein, and nerve pass to the anterior region of the thorax. Both lower and upper borders of the shaft give attachment to intercostal muscles.

Ribs are confined to the thoracic region in mammals. Occasionally a cervical rib persists in man and may lead to serious disturbance by pressure upon the brachial plexus.

In the cervical, lumbar, and sacral regions of mammals the homologues of ribs occur as costal elements fused with the transverse processes of the vertebrae (Fig. 81). The foramina traversed by the vertebral arteries and veins in mammals represent the openings retained between the vertebral transverse processes and the necks of cervical ribs whose vertebral ends have become fused with these processes.

THE PAIRED EXTREMITIES

The question of the origin of paired vertebrate extremities has been the subject of widespread inquiry and discussion, particularly during the last century, by such figures as Gegenbaur, Dohrn, Huxley, Balfour, Mivart, and Thacher. Even today, the subject has not lost its interest to the paleontologist or to the comparative anatomist. As recently as 1941, William K. Gregory and the late Henry C. Raven, both of the American Museum of Natural History, published an excellent study on the origin and early evolution of paired fins and limbs. From the mass of studies and observations, three theories about the origin of the appendages and the pectoral and pelvic girdles have crystallized. One, the Gegenbaur theory, assigned to the posterior cartilaginous gill arches and their assumed subsequent displacement the role of forerunner of pectoral and pelvic appendages. The evidence has not supported this view, and today it is primarily of historic interest (Fig. 82). The second, known as the Thacher-Mivart theory, although Balfour, Haswell, and Dohrn contributed to it, assigns to the lateral skin folds the origin of paired fins. These lateral skin folds, first noted by Balfour, are prominent in *Amphioxus* and appear in the development of the elasmobranchs, where segmental muscle buds may be associated with them. Their skeletal supports are presumably derived just as are those of the medium fins (Fig. 83).

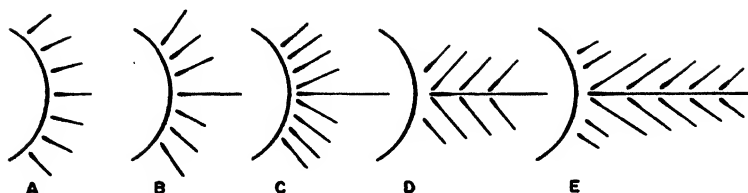


FIG. 82. To illustrate the Gegenbaur theory of the development of the biserial archipterygium. A, branchial arch with cartilaginous rays. B, C, and D, gradual preponderance of middle ray. E, secondary alignment of cartilages from the middle ray.

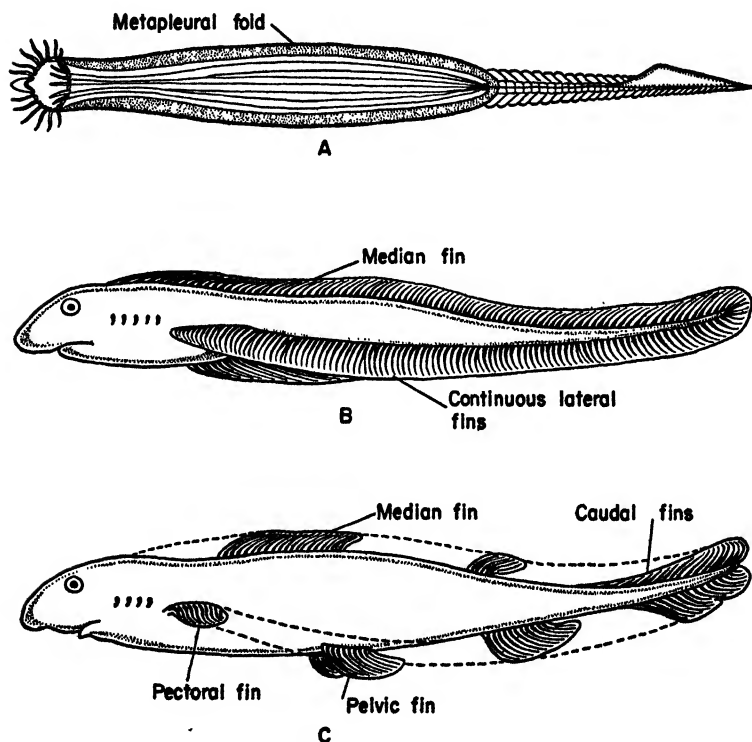


FIG. 83. The metapleural folds and their hypothetical reduction. According to the Thacher-Mivart theory, fins developed as the result of interruption of continuous fin and folds. A, the metapleural folds in *Amphioxus*; B, hypothetical chordate; C, median, caudal, pectoral, and pelvic fin arrangement in modern fishes. (Redrawn from various sources.)

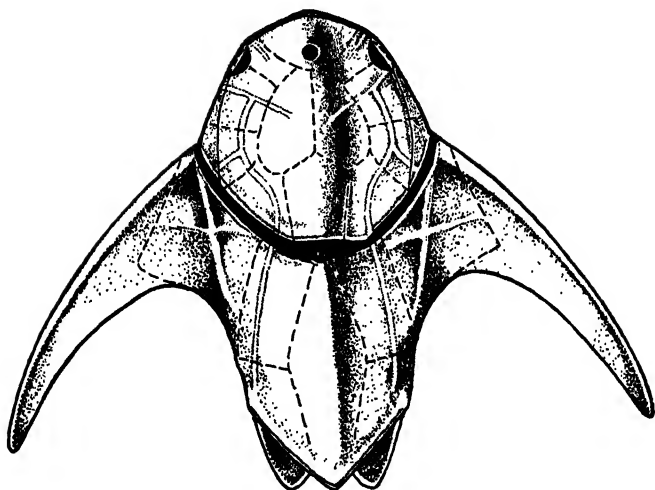


FIG. 84A. A primitive arthrodire (placoderm). Lateral spines at the pectoral level. According to Gregory and Raven, the covering plate of the pectoral girdle of fishes was derived by reduction from the thoracic armor of ostracoderms, which presumably gave rise to the placoderms. (Redrawn from Romer.)

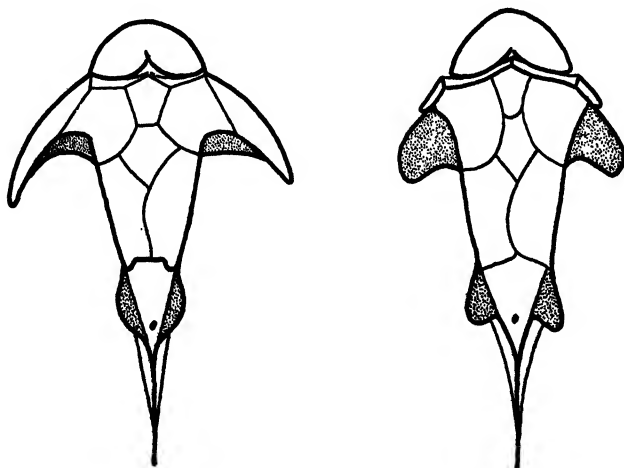


FIG. 84B. Suggested reduction of pectoral spines and development of membranous folds at the pectoral and pelvic levels, with the outgrowth of radials in the cephalaspidomorph ostracoderms. (Redrawn from Gregory and Raven.)

Recently Gregory and Raven advanced the theory that paired fins are derived by reduction of the thoracic armor of the ostracoderms (Fig. 84, *A* and *B*). In their words: "The covering plates of the pectoral girdle of the placoderms and true fishes have been derived by reduction from the thoracic armor of ostracoderms, just as the covering plates of their skulls have been derived from the cephalic plates of ostracoderms." The endoskeletal portion of the shoulder girdle of fishes, they believe, is an outgrowth from the basal pieces of the pectoral fins. Their extensive comparative study of the ostracoderms (fossil, prefish), placoderms (an extinct group of armored fishes), and earlier elasmobranchs suggests that both pectoral and pelvic girdles

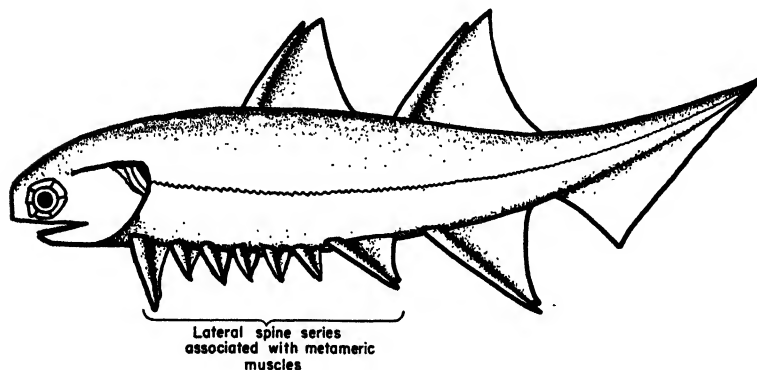


FIG. 85. Wide-based fin spines in the Anaspida (*Climatius*). Note that the spines form a series beginning with the pectoral and ending with the pelvic. These dermal projections were connected with metameric muscles of the flanks. (Redrawn from Romer.)

were once connected by intermediate spines and nodes, somewhat as in certain acanthodians (extinct, spiny elasmobranch fishes), *e.g.*, *Climatius* (Fig. 85).

In a study of the early evolution of the fishes, Alfred S. Romer states:¹ "In addition to median fins the acanthodians possessed unquestioned paired fins corresponding to the pectoral and pelvic appendages of higher fishes and land vertebrates. They were, however, built upon a peculiar pattern. Each bore at its anterior margin a stout spine. Behind the spine, in some cases, there are preserved traces of a web of skin forming a fin membrane; and in this region there are sometimes—

¹ *Quarterly Review of Biology*, Vol. 21, p. 46, 1946.

but very exceptionally—found remains of parallel bars forming skeletal fin supports. Still another peculiarity is present. In all higher vertebrates paired fins are restricted to two pairs, pectoral and pelvic, corresponding to the four limbs of land vertebrates. All acanthodians have these two pairs. But in all cases additional paired spines, interpreted as accessory pairs of appendages, are present between the pectoral and pelvic ones; in one genus as many as seven pairs were present. In the early days of 'experimentation' in the development of limbs it would seem that vertebrates had not, so to speak, made up their minds as to the number of limbs appropriate to them and that considerable variation may have existed before they settled down to the orthodox number of two pairs." Gregory and Raven believe that the most primitive true fish "is not the long-bodied spineless shark, *Cladoselache* of the Upper Devonian, but some form of the older, short-bodied, broad-spined acanthodians, such as *Diplicanthus*." The view that some "hypothetical primitive vertebrate with continuous finfolds" was the ancestral type is, according to them, an anachronism although it continues to persist in some textbooks.

Amphioxus is without paired fins, although from the anus forward along the lateral sides of the trunk paired metapleural folds extend to the head and a dorsal median skin fold with connective-tissue supports, or rays, extends the length of the body and passes around the tail to terminate just beyond the anus (Fig. 16).

In cyclostomes only median fins are found, one dorsal and centrally placed, the second continuous with a tail fin which encircles the caudal end of the body (Fig. 17). They are supported by cartilaginous rays, the latter associated with radial muscles. Whatever the origin of paired fins, we find them first at the elasmobranch level in living vertebrates.

Girdles. *Pectoral Girdle, Elasmobranchs.* The pectoral girdle of an elasmobranch, *e.g.*, the dogfish, consists of a cartilaginous, U-shaped, inverted arch whose free ends extend dorsally. The base of the arch, or *coracoid bar*, lies ventrally, and at its upper limit the *glenoid fossa* articulates with the fin (Fig. 86A and B). Extending dorsally from the articulation, another cartilaginous process, the *scapula*, may end in a *suprascapular* process. Both pectoral and pelvic cartilaginous supports originate as segmental endoskeletal structures (pterygiophores). Their subsequent division results in the formation of basal and radial cartilages. Secondary fusion of the basals and the extension of the anterior ones to the midline form the cartilaginous coracoid and pelvic bars.

Pelvic Girdle, Elasmobranchs. In the elasmobranchs, dorsal extensions comparable with the scapulae in the pectoral girdles occur also in the pelvis; these are the *iliac processes*. Segmental muscle buds associated with the endoskeletal cartilages attach to the lateral and

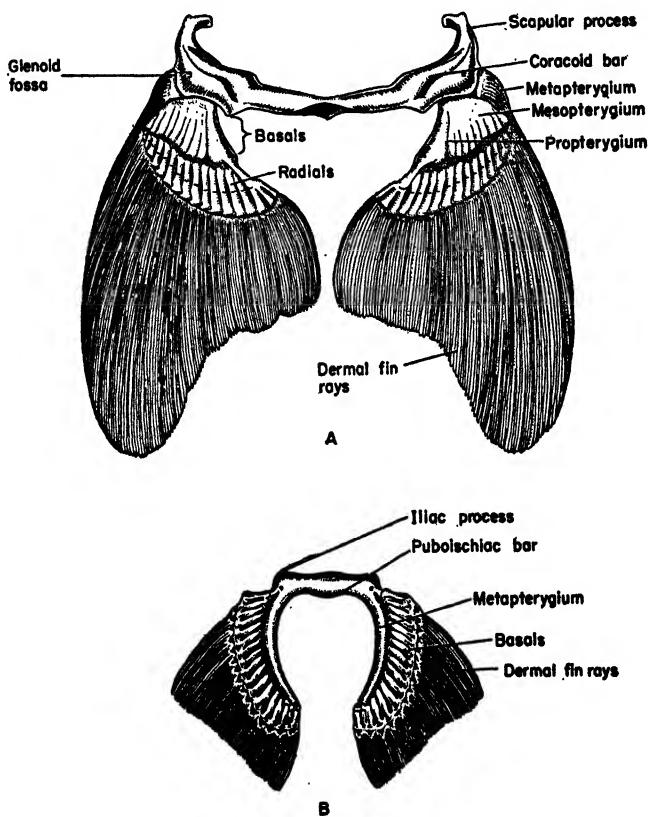


FIG. 86. A, elasmobranch pectoral girdle and fins. B, elasmobranch pelvic girdle and fin.

medial surfaces of the radial cartilages and furnish the first means for abduction and adduction of the appendages. The innervation, likewise segmental, follows these muscular slips and shows the beginning of plexus formation by the junction of the first nerve in the series, the collector, with the succeeding nerves.

Pectoral and Pelvic Girdle, Bony Fishes. The cartilaginous mechanism described above is the primary girdle. Elasmobranch girdle development stops at this level. With ossification of the skeleton in the teleostomes further changes also modify the girdles. A secondary dermal girdle arises from ossification in the skin and results in the formation of several bones (Figs. 87, 88). Most ventrally a *clavicle* unites the girdle with the sternum, while dorsally a *cleithrum* supports the articulation; the latter may be joined by a *supracleithrum* and a *posttemporal* bone, which extend the shoulder girdle to the head. When present,

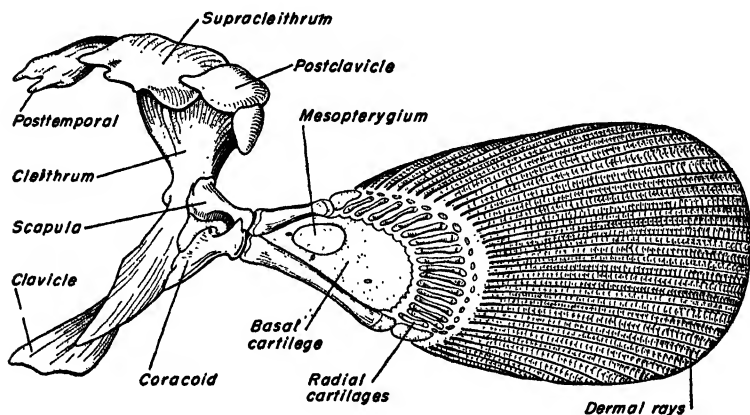


FIG. 87. Right shoulder girdle of *Channa*, a teleost fish. The posttemporal, supracleithrum, and cleithrum are retained, in addition to clavicle, coracoid, and scapula. Posttemporal and cleithral elements are discarded in amniotes. (After W. K. Parker.)

the posttemporal lies between the supracleithrum and the skull and joins the girdle and head. The new bony girdle also becomes increasingly associated with trunk muscles, as the primary girdle is pushed into the background. The cleithrum may migrate ventrally and cause the disappearance of the clavicle. While the primary girdle is reduced, it does not become extinct. Ossification of the coracoid bar transforms it into the coracoid bone, with a similar transformation in the scapula.

Pelvic changes are homologous to this evolution of the pectoral girdle, although not so pronounced. The proximity of this girdle to the tail has undoubtedly been a factor in its retardation. The dermal plates which play such a prominent role in the development of the secondary girdle are not prominent in the pelvic girdle. In teleostomes, partial

ossification of the primary pelvic plates becomes completed in the teleosts, where the two pelvic plates commonly are joined. As in the pectoral girdle, definite muscle slips cover the lateral and medial aspects of the radial cartilages beyond the basal, which are usually reduced to a single element. Basal and radial elements are ossified, just as are the girdles.

Free Appendages. Fishes. The girdles are the foundations for the free appendages. Considered from a functional standpoint the end to be served by evolution of a girdle is the support it gives to fin, flipper,

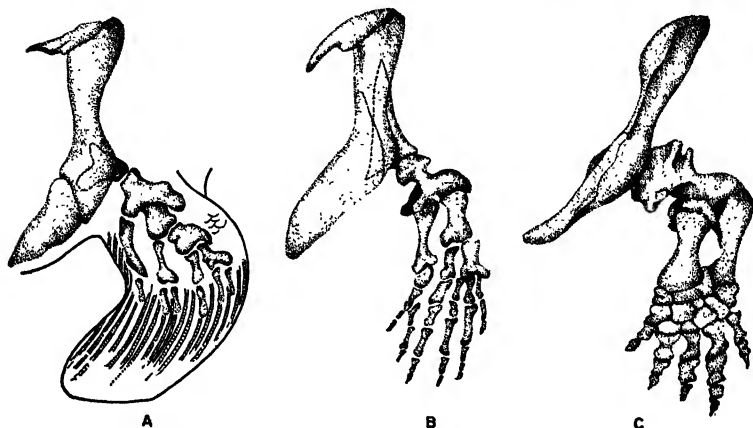


FIG. 88. Transformation of crossopterygian pectoral girdle and paddle into pentadactylate type. Gregory's theory. Oblique front view of left side. A, *Eusthenopteron foordi*; B, *Eogyrinus* and partly hypothetical intermediate; C, *Eryops megacephalus*. (Redrawn from Gregory and Raven.)

wing, arm, or leg. It is the free extremity that makes functional contact with water, earth, or air. With the gradual transformation of the appendage from a balancing organ in water to a weight-bearing leverage system on land, profound changes have involved the musculature perhaps even more than the skeleton, once the underlying skeletal pattern had been established.

It is axiomatic that pectoral and pelvic fins bear a close structural resemblance to each other; the phenomenon is known as serial homology. They also resemble the median unpaired fins. In contrast, however, to the broad base which results from the parallel arrangement of the radial cartilages which support the median fins, the base of the paired fins is narrowed and articulates with the pectoral or pelvic girdle, as the case may be.

The so-called *biserial archipterygium* described by Gegenbaur and present in the extinct pleurocanths and ancient elasmobranchs, as well as in the crossopterygian fishes and modern Dipnoi, originated from a narrow elongate base with radial cartilages extending on either side like the ribs of a leaf (Fig. 82). A modification and possible derivation of this type is the *uniserial archipterygium*, more frequent in the pelvic appendages. Here the radials extend only from one side of the basal cartilage.

The lungfish *Ceratodus* has retained the primitive type of biserial archipterygium both in its pectoral and pelvic appendages. A central axis of cartilages extends to the tip of the fin, articulated radial cartilages on either side of this axis becoming smaller toward the periphery. The arrangement of these latter cartilages is not entirely symmetrical, since the dorsally directed are more plentiful than the ventrally placed ones. In *Protopterus*, another dipnoan, the radials have disappeared, and only the long central axis of cartilages remains to support the slender, whip-like fin.

The typical pectoral fin in modern elasmobranchs consists of three basal cartilages of varying size, a *propterygium*, *mesopterygium*, and *metapterygium* articulating with the shoulder girdle (Fig. 86). Joining these basal pieces distally are a varying number of *radial cartilages* each of which may consist of several shorter segments, and extending beyond these to the periphery are delicate *dermal fin rays* embedded in the skin. Present-day elasmobranchs show only the uniserial type of fin, and in this type the metapterygium becomes the dominant basal cartilage. The pelvic appendages show homologous development with the pectoral; in male elasmobranchs, however, the metapterygium is extended by addition of cartilages and becomes a copulatory organ. The remaining two basal cartilages become greatly modified or lost. In the extinct pleuracanth, which were fresh-water elasmobranchs, a biserial pterygium occurred.

In ganoid and teleost fishes the fin supports may be partly cartilaginous and partly of bone. Bony elements are added from the integument, thus forming a secondary skeleton, while the original cartilaginous elements may also be converted to bone. There is a further reduction of the basal elements, although as many as five basal cartilages are laid down in the embryo. A variable number of radials distal to the basals appear in the ganoids. These may also be partly of cartilage and partly of bone. In the teleost, or bony, fishes the cartilaginous radials are overlaid by secondary skeletal elements of bone.

The pelvic fins of ganoids are greatly reduced in comparison with the pectoral. A metapterygium to which are joined several radial

cartilages distally persists. In *Polypterus*, one of the bony ganoids, four bony radials articulate with the metapterygium, while in *Lepidosteus* they may disappear entirely. In the teleosts there is complete conversion of the metapterygium with a migration of the right and left metapterygia medially, resulting in a symphysis-like approximation along the midline. Distally small cartilaginous or bony radials may be present, although in many species they disappear. Dermal fin rays persist in both the ganoids and the teleosts.

We have assumed, with Gregory and Raven, that pectoral and pelvic girdles may have arisen from horizontal spines, or nodes, which formed a series of paired projections comparable with those in the acanthodian sharks. This type of shoulder girdle arose apparently "when the endoskeletal basal pieces of the pectoral fin worked their way farther into the body and encountered the transverse septum behind the pericardium." The dermal plates of the girdle, according to these authors, represent remnants of a primitive thoracic exoskeleton. The pelvic girdles lagged in comparison with the pectoral. Dermal plates were usually lacking in this girdle, and the ostracoderms failed to show any traces of cartilaginous skeletal parts in the skeletal fin.

EVOLUTION OF LAND APPENDAGES

How may the land appendages be developed from the fin, or must we assume their independent evolution? It may be stated categorically that it was not an independent development, since there are definite transitional forms between aquatic and land types. It seems necessary to choose an ancestor for the Tetrapoda, or four-footed animals. In the past, both dipnoan and crossopterygian fishes were considered, since, aside from the possession of open swim bladders capable of functioning as lungs, they had other transitional features, including lobed fins and internal nares.

Evidence supports the view that the crossopterygian fishes are ancestral to land vertebrates (Fig. 88). In the course of their extensive study of the crossopterygian fish *Eusthenopteron*, Gregory and Raven recently examined a number of collections of this fossil. The secondary pectoral girdle, the clavicle-cleithrum, is well developed; the primary, a scapula-coracoid, is in their words "small and rarely preserved." The pelvic rod is narrow with a pointed pubic tip, a caudally placed acetabulum without an ischial extension. They observed a posteriorly directed process that they consider the homologue of the ilium. They suggest a derivation of the primitive amphibian appendage from the *Eusthenopteron* type. Supporting this concept is the arrangement of

the proximal basal and the distal radial elements. A single bone, the homologue of the humerus, articulates with the shoulder girdle; paired distal elements correspond with the radius and ulna. To account for the development of the carpals, metacarpals, and phalanges, they consider the proliferation of the "digitiferous zone." As a result of increasing use of the paddles for the support of the body weight, they believe that a "sharp flexure line would be developed between the fin ray web and the fleshy lobe." In this way the "digitiferous zone" would gradually be the locus of the converging stresses of the flexor and extensor surfaces; it would become the main zone of contact between the fin and the ground. As the muscular lobe extended periph-

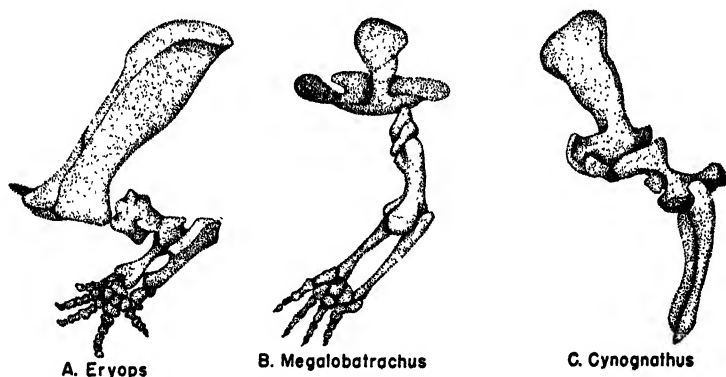


FIG. 89. Primitive and later positions of limbs. A, ancestral amphibians; B, primitive amphibian; C, mammal-like reptile. (Redrawn from Gregory and Raven.)

erally, its skeleton became subdivided into five emarginated projections from which the future carpals (tarsals), metacarpals (metatarsals), and digits developed. As these skeletal parts evolved they carried with them especially the tendons of the flexors and extensors that are inserted in the terminal phalanges.

The transition from water to land limbs involved more than changes in the girdles alone. With this transformation came the invention of elbow, knee, wrist, and finger joints. The accompanying Figs. 88 to 90 in this text show the hypothetical steps in this transformation. The new uses to which the limb was put in climbing over muddy bottoms and in supporting the body on land are assumed to be the causal factors in creating it. This would imply that use was responsible for its creation, although from a biological standpoint this view is un-

tenable. The underlying assumption is that a group of crossopterygian fishes happened to possess lobed fins and were in a position to give rise to mutants with new anatomical features in girdles, appendages, and other characteristics which led to the Stegocephalia. Gregory and Raven maintain that the wholly new habit of using the paired appendages to support the weight of the body on land became possible only through a drastic revolution in construction, with the loss of many ancient uniformities and the rise of such new and unexpected entities as the digitiferous zone on the margin of the rhipidist "fleshy lobe."

Amphibia. The most primitive land limbs are found in the extinct Stegocephalia (Fig. 25). The limbs are extended at right angles to the long axis of the body, placing the short humerus and femur in an ap-

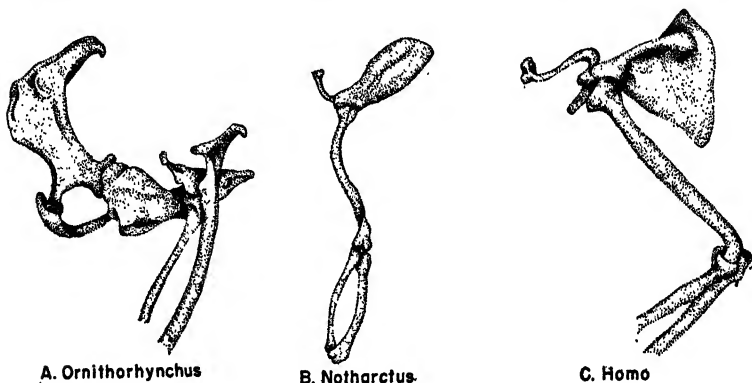


FIG. 90. Position of limb in A, monotreme; B, primitive primate; C, man. (Redrawn from Gregory and Raven.)

proximately horizontal position. Both bones are massive, offering wide surfaces for muscle attachments.

The humerus has large radial and ulnar epicondyles to which the extensors and flexors of the wrist and hand presumably were attached (Fig. 88C). Radius and ulna were well defined and slender in comparison with the short, broad humerus in *Eryops* (a genus of large stegocephalians). Wristbones were not completely ossified, and movement appears to have been limited, since the articulations are syndesmotomic in character. Some 11 carpal and 12 tarsal bones supported four digits in the hand and five in the foot, respectively. Claws had not yet appeared.

The Pectoral Girdle. The shoulder girdle, ossified at least in part, contained both primary (coracoid, scapula) and secondary (clavicle,

interclavicle, cleithrum) elements. An interclavicle joined the two clavicles midventrally and apparently was an adaptation for holding the girdle firmly in place because of the tendency for the shoulders to be pulled apart ventrally by the weight of the body. The cleithrum was reduced, which is also true of the scapula in some *Stegocephalia*; in others it was entirely cartilaginous. In the large forms it was broad but without a spine or acromial process.

The pelvic girdle of the *Stegocephalia* was a ventral plate combining pubic and ischial parts and joined in the midventral line. A dorsally directed ilium joined the other two bones in an acetabulum of considerable depth. These parts were ossified in the large representatives.

In the living anuran *Amphibia*, the shoulder girdle is firm and narrow (Fig. 75). The coracoid, to which is joined anteriorly a cartilaginous procoracoid, is separated from the coracoid of the opposite side by epicoracoid cartilages. The latter may overlap in the median line. The scapula, large and commonly ossified, is frequently extended dorsally by a suprascapula in a cartilaginous or calcified state. The secondary girdle, small in comparison with that of the *Stegocephalia*, has a narrow clavicle that overlies the cartilaginous procoracoid process. A cleithrum is generally absent, but when present it extends along the anterior margin of the suprascapula. A well-developed sternum and xiphisternum extend caudally from the epicoracoid cartilage; an omosternum lies cranial to it. In urodeles the coracoid is a thin, broad cartilaginous plate, extended dorsally as the scapula; a cranial extension of the plate forms the procoracoid cartilage. Ossifications occur in the scapula, coracoid, and procoracoid. A secondary girdle is absent, presumably associated with the aquatic habit and the consequent lesser demands for support of the body weight.

The Pelvic Girdle. In *Anura* the pelvis is characterized by great length and forward extension of the ilium and by its articulation with the sacral cartilage. This is due in part to the anterior displacement of the sacrum. The ventral part of the girdle is compressed and flattened; ischium and ilium are ossified, as is also the small pubis. Both an epipubis and a postpubis may be associated with the girdle, the one extending cranially, the other caudally. The urodeles have a cranially directed, Y-shaped epipubic cartilage developed in the linea alba but associated with the pubis.

Free Appendages. The free appendage of modern *Amphibia* is far removed from that of the fishes (Fig. 91). No direct transitions between the two types have been found, and comparative anatomy has had to resort to hypotheses in addition to utilizing the meager evidence

that might point to the nature of changes that led from one to the other. What evidence there is points to a reduction of the cartilaginous or bony elements constituting the forerunner of the land appendage. With this appeared a serial arrangement of the bony segments, one proximal, two distal, and a variable number of carpal (tarsal), meta-

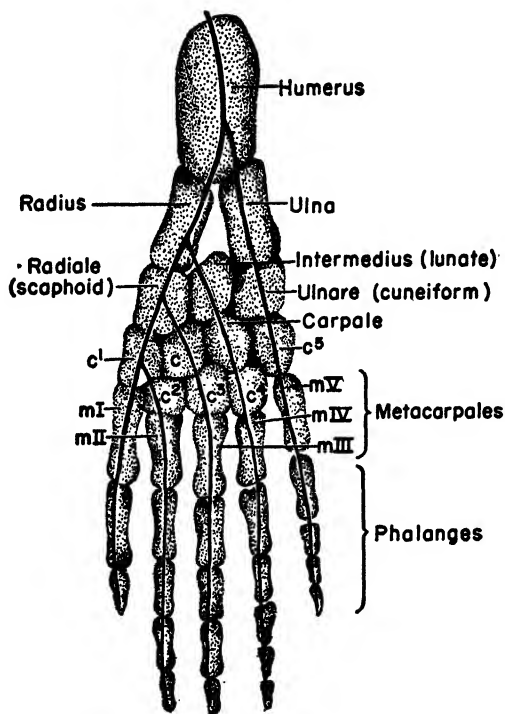


FIG. 91. Diagram of the free amphibian appendage, showing the generalized hand, which is retained in land reptiles and mammals with the exception of those which returned to aquatic life or were subjected to excessive specialization. (Redrawn from Bronn.)

carpal (metatarsal), and phalanges, peripherally. This pattern, already well established in the Stegocephalia, retains many of its generalized features in the Amphibia.

The urodeles, in spite of small size and aquatic habits, show considerable resemblance in their appendages to the much larger Stegocephalia. Wrist- and anklebones vary in number, largely as the result of variable

fusion. Digits usually number four in the hand and five in the foot. Associated with the water habitat, a simplification of the appendicular skeleton may occur to such degree that the limbs no longer support the body on land, as in *Typhlomolge*, the cave-water-inhabiting amphibian found in the southwestern United States.

In the Anura, associated with the jumping habit, modifications have affected not only the axial but the appendicular skeleton. In the forelimbs the elbows are bent outward, and the hand is maintained in a prone position. The four digits have a varying number of phalanges; in the frog they number 2,2,3,3. In some of the tree frogs, addition of vacuum cups on the fingers has associated with it an additional phalanx on each of the fingers. Radius and ulna are fused. In the anuran hind limb, adaptation to the saltatorial habit is evident in the elongate, slender femur; the fused and equally long tibia and fibula called the *os cruris*; lengthening of two of the tarsal bones, the tibiale and fibulare, fused at their ends and constituting an additional lever system; reduction of the remaining anklebones; retention of five elongate digits with 2,2,3,4,3 phalanges, respectively. The fourth is the longest digit. Webs between the digits and the metatarsals or the metacarpals make a truly amphibian or dual locomotor organ of the hands and feet, *i.e.*, they serve both on land and in the water. Claws or foot pads mark the terminal digits. The former, it will be recalled, are an amphibian invention.

Reptiles. *The Pectoral Girdle.* The reptilian pectoral girdle is also related to that of the extinct *Stegocephalia* (Fig. 92). The primary girdle is large and ossified; the secondary is prominent. It will be recalled that the primary comprises a coracoid and scapular bone to which may be added other coracoidal and scapular elements, and that the secondary consists of clavicle and cleithrum, to which may be added inter- and proclavicular elements and supracleithra, or supratemporal segments. In the oldest reptiles (*Cotylosauria*), represented only by fossils, the primary girdle is united into a scapula-coracoid. In *Seymouria*, a primitive extinct reptile, the bones are separated and procoracoid and coracoids are present. The humerus retains its primitive horizontal position as in the *Stegocephalia*. An interclavicular bone joins the medial ends of the clavicles; this probably represents an adaptation for supporting the body weight. A small cleithrum occurs.

In the extinct reptiles, shoulder-girdle development was correlated with its special uses. In the great dinosaurs, in which the hind limbs frequently became the only organs of locomotion, the shoulder girdle is simplified, the secondary girdle has disappeared, but coracoid and scap-

ular elements are retained and may be fused with each other. In the Archosauria, on the other hand, in which the shoulder girdle and pectoral appendage became adapted for flight, scapula and coracoid became elongate, and the glenoid cavity moved dorsally. Ventrally the girdle was made firm by the joining of the clavicles to form a *furcula* and by a *carina*, or keel, to which the furcula was joined by a ligament, as in

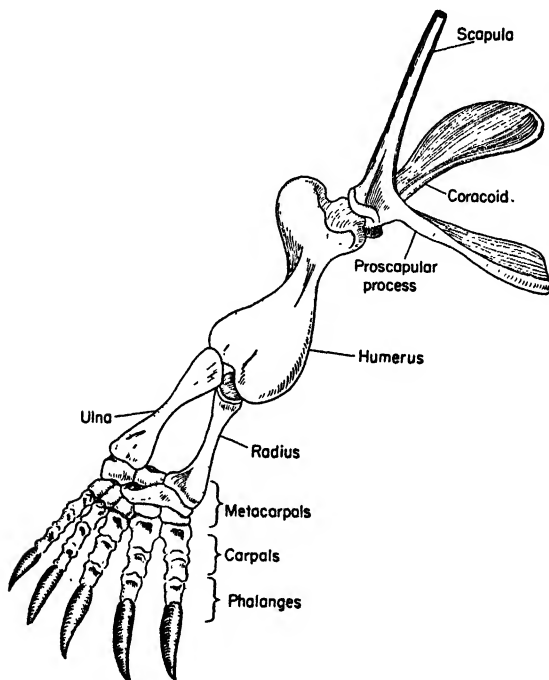


FIG. 92. Shoulder and appendage of turtle. The reptilian limb has a short massive humerus; the distal end of the extremity remains generalized.

modern birds. The Plesiosauroidea, which returned to the water, used the appendages for swimming, and associated with this function we find heavy bony coracoid and clavicular plates in the girdle, while the scapula was reduced.

In *Sphenodon*, a primitive living reptile, many early features of the extinct *Cotylosauria* are retained. In the remaining lizards, the small active *Lacertilia*, the demands on the shoulder girdle lessened, and correlated with this condition the primary shoulder girdle is reduced.

The coracoid is plate-like, uniting medially with its fellow by a cartilaginous epicoracoid process or by a cranial extension of the sternum. The scapula is small and has a dorsal cartilaginous or calcified extension, the suprascapula. The narrow clavicles join the medially placed interclavicle on each side; a cleithrum is absent.

The crocodilian girdle bears a superficial resemblance to the lacertilian. The primary girdle consists of a coracoid and a scapula, with a well-defined glenoid cavity at their junction. Both bones are relatively large and completely ossified. A suprascapular cartilage joins the vertebral margin of the scapula. The secondary girdle, reduced to an interclavicle, overlies the greatly developed sternal plate in the mid-ventral line. The clavicle has disappeared, a condition probably traceable to the ancestry of the crocodilia, the Pseudosuchia, in which many representatives used only the hind limbs for locomotion.

The Chelonians have a unique shoulder girdle, correlated with the great exoskeleton (Fig. 92). The primary girdle (coracoid-acromion-scapula) has become lodged inside the rib basket; the secondary girdle (clavicle and interclavicle) is fused with the exoskeleton as epi- and entoplastron.

The Pelvic Girdle. The reptilian pelvic girdle is correlated in its development with the demands made upon it in locomotion. The hind limbs in land animals, by their pushing action, are the prime movers of the body. The pelvis has responded to these demands. It is joined in the reptiles to the sacral vertebrae by two sacral ribs. It has increased its surface, thereby offering greater attachment to the muscles of propulsion. The reptilian pattern apparently, as noted, evolved from the stegocephalian, where a pubis, essentially of two ventral plates, united with a dorsally directed ilium. The latter joins the sacral vertebrae by a broadened sacral rib. All three elements, pubis, ischium, and ilium, were ossified, except in some small stegocephalians, where the pubis failed to develop. The ancient reptilian Cotylosauria had a similar plate-like pubis, joined with its fellow in the midventral line with a dorsally directed ilium, the latter joined with the sacrum by two sacral ribs, indicating differentiation of two sacral vertebrae.

In modern reptiles, *Sphenodon* has a pubis and ischium directed medially and separated by a large obturator foramen. Pubis and ischium are united by a cartilaginous symphysis. In the crocodiles the bones of the pelvis are ossified, the pubes forming a symphysis, while the ischia are directed caudally and may also join each other.

Turtles exhibit a wide ventral symphysis of pubis and ischium; the ilium is relatively small and directed dorsally and medially.

In the archosaurians, the extinct reptilian group that presumably

gave rise to flying reptiles, which in turn evolved the birds, a possible transition to the avian pelvis has been observed. In *Euparkeria*, for example, the pubis is bent caudally, while both ischium and ilium are directed anteriorly. In *Iguanodon*, another bird-like reptile, the slender-

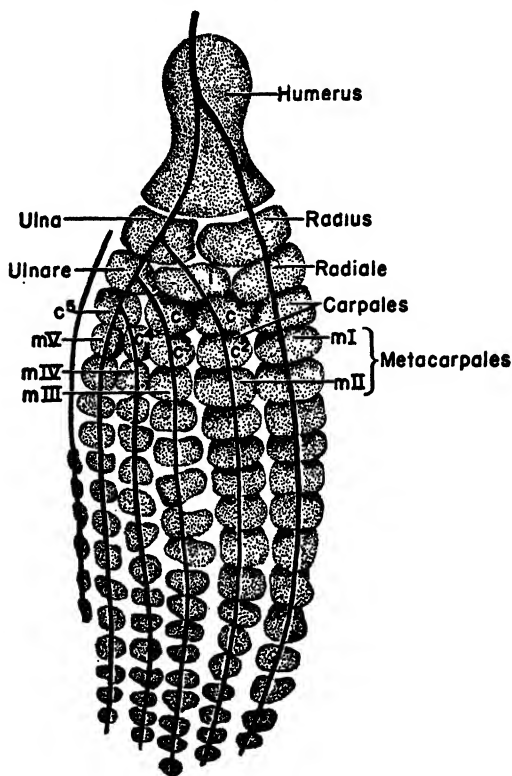


FIG. 93. Free appendage of *Ichthyosaurus*, an extinct, fish-like aquatic reptile. Note the small forearm and hand bones, forming wide support to the paddle. (Redrawn from Bronn.)

ized pelvis is completely caudal in its direction and lies parallel to the ischium. In *Apteryx*, the primitive nonflying bird, the definite avian girdle emerges.

Free Appendages. In the ancient cotylosaurian reptiles the appendicular bones are relatively short and heavy. The humerus and the bones of the forearm retain their horizontal position with reference to

the body axis. The humerus, relatively short and expanded both at the proximal and the distal ends, frequently has foramina in the radial and ulnar epicondyles, traversed by the radial and by the ulnar nerve and the brachial artery, respectively. *Sphenodon* among the living reptiles retains these foramina.

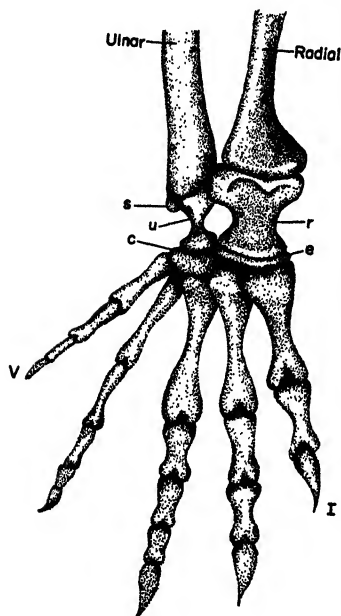


FIG. 94A.



FIG. 94B.

FIG. 94A. The hand of the alligator. Wristbones are reduced in number. The generalized hand is retained. (*Redrawn from Bronn.*)

FIG. 94B. The human hand. Eight carpals, 5 metacarpals, and 14 phalanges constitute the skeletal support for the hand.

In living reptiles the forearm assumes a more vertical position; the head of the humerus is a half sphere; the bone elongates. A lateral and a medial process are retained at the proximal end; the former, marking the insertion for the deltoid and pectoral muscles, is represented by the deltoid tuberosity in mammals. An olecranon process appears at the proximal end of the ulna. Wrist and hand articulations are slightly developed; the wrist bones are generally ossified, except in the water inhabitants (Figs. 93, 94A). The original large number of

wristbones is reduced in modern Crocodilia to three proximal ones, a tibiale, intermedius, and ulnar, which articulate with the distal ends of the radius and ulna, and three to four centralia, distally fused with them. Five-clawed digits mark the termination of the upper limb.

Reptilian pelvic appendages are usually longer and heavier than the pectoral. The femur, horizontally placed and closely approximated to the body, in comparison with the extinct Reptilia, is more slender and elongate. Forerunners of the trochanters are represented by the Y-shaped adductor crests at the proximal end of the femur. The tibia, medial to the smaller fibula, bears most of the body weight. At the knee its two articular facets meet the two condyles of the femur. The fibula, tied to the tibia at its proximal end, articulates with the lateral condyle of the femur. The foot has two or three proximal bones and originally had two centralia, which may be reduced to one. The distal tarsals may be fused with the metatarsals. An intertarsal articulation permits greater dorsiflexion of the foot. Four metatarsals and a vestige of the fifth are common. Associated with these distally are four or, frequently, five digits.

Birds. *The Pectoral Girdle.* The pectoral girdle in birds shows distinct resemblance to the reptilian (Fig. 95). The furcula (clavicles, wishbone), which first appeared in the Archosauria, is retained. A heavy, short coracoid joins the greatly expanded carina, or keel, another feature held over from the flying reptiles. Precoracoid and scapula continue the resemblance; the scapula, elongate and blade-like, is pushed well over the dorsum. The carina, greatly expanded in the flying birds, gives wide attachments to the great pectoral flight muscles; it also lends firmness to girdle and rib basket, qualities essential for the new and enlarged functions of the anterior limbs in the birds.

The Pelvic Girdle. The avian pelvic girdle extends both anteriorly and posteriorly along the vertebral column. This is due to both forward and backward extension of the ilium and the retention of the prepubis. Ischium and pubis are caudally directed, and with the exception of Struthio the pelvis is open ventrally; in other words neither pubis nor ischial symphyses are formed. In the ostrich, however, a posterior extension of the ischium forms a symphysis dorsal to the intestine, while ventrally and caudally a pubic symphysis may occur beneath intestine and cloaca. Other secondary junctions between ischium and pubis and between ischium and ilium may arise. Loss of the ventral symphysis is generally attributed to the habit of laying hard-shelled and large eggs. Characteristic, also, of the bird pelvis is the extensive fusion of the pelvis with the fused vertebrae of the sacrum.

Free Appendages. Birds, in comparison with reptiles, exhibit great modifications in their free appendages, particularly in the wing. The girdle is securely anchored to the keel as indicated; the humerus is relatively long in the good fliers, as are also radius and ulna. The wristbones are reduced to a radial and fibular, while the remaining carpal bones are fused with the metacarpals. Three metacarpals are formed, the third the largest and the second fused with it, while the first is vestigial. Phalanges tipped with claws are associated with the metacarpals.

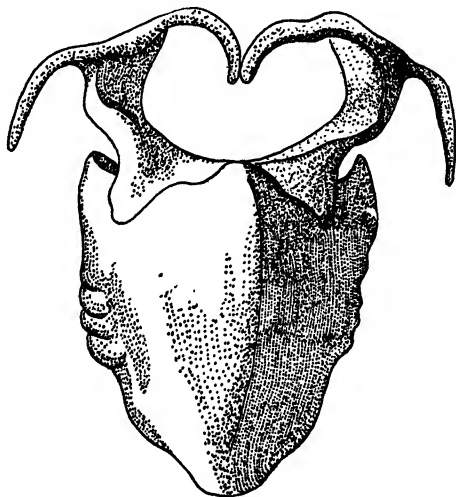


FIG. 95. The pectoral girdle of the carinate bird is securely braced to the greatly expanded sternum, or keel. The furcula, or wishbone, represents an additional support.

A peculiar feature of many bones of carinate birds is their hollow nature, associated with loss of spongy bone. These pneumatic bones contain extensions of the air sacs, which in turn are confluent with the bronchi. The chief advantage of this development is reduction of skeletal weight and increase in vital capacity.

In the hind limb the femur is relatively short, and the knee is brought forward. A greater trochanter is prominent. A patella is associated with the bipedal position and the maintenance of balance. The appendage becomes free beyond the knee. The tibia, the largest leg bone, bears the weight; the fibula is vestigial, and while proximally it articulates with the femur, distally it ends as a fine, bony sliver before

reaching the foot. The first tarsal bone fuses with the tibia. The first metatarsal is vestigial, the second, third, and fourth bear the weight, while a fifth is lacking. In ostriches the toes are reduced to two (Fig. 58C); in some other birds they are reduced to three. The first toe when present is directed posteriorly and is opposable.

Mammalian Girdles. *The Pectoral Girdle.* The forerunners of the mammals, the theromorph reptiles, had a shoulder girdle in which the primary elements were a pro- and metacoracoid and a scapula. The metacoracoid was frequently reduced or absent. In modern reptiles this has entirely disappeared, and the coracoid bone of these groups corresponds to the procoracoid of the primitive Cotylosauria. (Some of the later theromorphs, Anomodontia, developed a spine as well as an acromion on the scapula.) The secondary (dermal) part of the girdle of the theromorphs comprised a clavicle, interclavicle, and cleithrum. The theromorphs were an extinct reptilian group intermediate between labyrinthodont amphibians and monotreme mammals.

The monotremes, most primitive of mammals, retain the same elements in the shoulder girdle which were present in the theromorphs. The interclavicle articulates medially with the clavicles, and the sternum remains caudal to it and does not join with the clavicles.

In the marsupials the coracoidal and interclavicular elements have regressed. The clavicle now articulates medially with the sternum; laterally, with the acromion of the scapula. Associated with the margin of the glenoid cavity and the shoulder articulation, the coracoid has fused with the scapula. The latter, relatively large, has a well-defined spine and acromion. The bone remains movable since dorsally its connections with the column are muscular and ventrally it articulates with the sternum indirectly through the clavicle. When the latter is absent, *e.g.*, in ungulates, the connections of the girdle with the axial skeleton are entirely muscular.

The sternum moves cranially in the true mammals, or Eutheria, and articulates with the clavicles.

Differences in the shoulder girdle of the various mammalian orders are small in comparison with reptilian. The clavicle disappears in some (ungulates), is rudimentary in others (carnivores), and is very large with secondary humeral articulation in some burrowing mammals (moles) with a second scapular spine, the spina posterior, associated with the greatly developed triceps brachii in these Insectivora. In primates it is a prominent skeletal link uniting the shoulder girdle with the sternum and supporting the head of the humerus.

The Pelvic Girdle. The mammalian pelvic girdle appears definitely

related to that of the anomodont theromorph reptiles (Fig. 79). Ilium, pubis, and ischium meet in the acetabulum. The ilium joins the column at the auricular articulation and is directed downward and posteriorly toward the acetabulum. The number of sacral vertebrae associated with the ilium have increased, compared with the two which articulate with it in the reptiles. A small acetabular bone, a part of the acetabulum, becomes fused with the pubic bone. A further characteristic of the mammalian innominate bone, or coxal bone, as the three fused hipbones are called, is the acetabular notch. At the mid-point of the notch or socket of the acetabulum a *ligamentum teres*, in life, ties the head of the femur to the innominate. This is in addition to the support offered by the capsule of the joint and its associated ligaments.

Right and left pubes are joined by a suture, the cartilaginous symphysis. In man and some other mammals, no ischial symphysis occurs; in others, *e.g.*, the rabbit and cat, both pubes and ischii join at the symphysis.

Marsupial bones extend cranially from the pubes in the Protheria and Metatheria. Presumably they support the pouch in these animals, but that function is questionable since in some (*Echidna*) they are not connected with it. In the Cetacea and Sirenia a pelvic girdle is vestigial or absent. The mammalian tail is generally reduced, compared with that of the reptiles, and this presumably has caused some modifications in the pelvis.

Free Appendages. As indicated earlier, the mammals probably arose from the primitive reptilian theromorphs. These had made a number of skeletal advances in the position of the limbs, which were carried farther under the body, so that the trunk was no longer slung between the pectoral and pelvic girdles. This permitted greater speed and greater efficiency in applying the power from muscles. Elbows and knees were sharply bent, and the shoulders approximated the sides of the body. In the cynodonts (dog-like reptiles) particularly, this approach to the mammalian position of the limbs was emphasized. Among living mammals the opossum probably approaches most closely the generalized reptilian limb pattern, although the monotremes in their shoulder and pelvic architecture show very primitive reptilian traits.

After the mammalian class had become established, further changes, many of them paralleling those in the various reptilian orders, occurred. Such changes modified the generalized pattern, which consisted of one proximal element, the humerus or femur; two distal bones, the radius

and ulna or tibia and fibula; a carpus of eight to nine elements or tarsus of seven to eight elements; five metacarpals or metatarsals, and five digits. These changes involved most frequently wrist- or anklebones and, secondarily, metacarpals, metatarsals, and digits, as well as slenderizing of the long bones.

In the monotremes the humerus is short and widened at both ends; forearm bones are short. The limbs approximate a horizontal position with reference to the long axis of the body. The fibula has a long proximal extension comparable with the olecranon of the ulna.

The marsupials, as indicated, are an ancient stock going back to the late Cretaceous period and contemporary with the last dinosaurs. Their skeleton indicates an adaptation to arboreal life, like the skeletons of some of the placental mammals. The limbs have been brought well under the body. The head of the humerus is convex, the bone slenderized, although its distal end is widened with a foramen for the passage of the ulnar nerve in the medial epicondyle. The radius articulates prominently with the capitulum of the humerus. The ulna has a well-defined olecranon. A considerable degree of supination of the forearm is possible. Both radius and ulna are about equally developed. The wrist is characterized by eight bones. Five metatarsals and five fingers, each tipped with a claw, make up the hand skeleton. A small prepollex is present.

The femur has a well-rounded head and greater and lesser trochanters. The fibula participates in the knee articulation. Seven anklebones with a prehallux, five metatarsals, and five digits characterize the ankle and foot. Claws are on all the terminal phalanges.

In the placental mammals there is great divergence in the type of limb, depending upon the habitus. Tree dwellers possess a high degree of supination and varying degrees of opposability of the first digit of hand or foot. The Carnivora, presumably derived from primitive tree inhabitants, exhibit reduced supination.

In the bears and raccoons the *plantigrade* foot persists. This, too, is generally a mark of arboreal inhabitants. In this type of foot the entire sole rests flat on the surface. In the swift runners the foot approached the *digitigrade* position, in which the animal was balanced on its toes. Characteristic of this group are the Felidae (cats) and Canidae (dogs); this development culminates in the *unguligrade* foot, or hoof, of the ungulates. Changes in the digits accompany modifications in locomotor habits. Reduction or shifting of toes occurs, whereby digits 3 and 4 lie forward of digits 1 and 5, with the latter reduced; and frequently, as in the cats and dogs, the first digit of the foot is absent.

In the ungulates this specialization for running has resulted in (1) the artiodactyl type of foot, in which digits 3 and 4 are dominant and carry most of the weight, while 2 and 5 are reduced or vestigial and displaced posteriorly; (2) the perissodactyl foot, in which the third digit carries the weight with varying changes in the others. Thus in the modern horse, 1,2,5 are absent as distinct bones; metacarpals 2

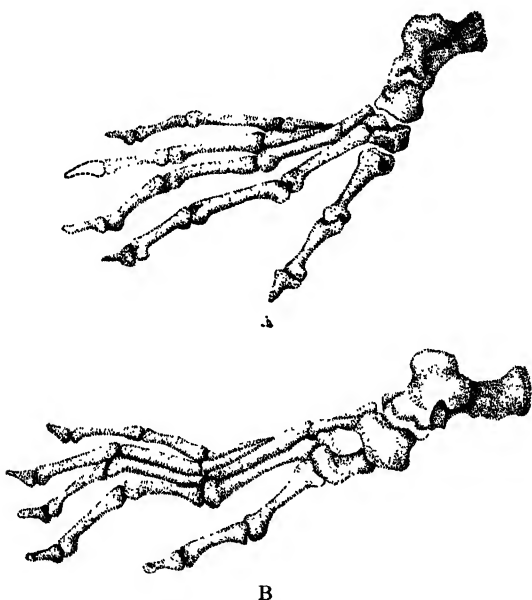


FIG. 96. *A*, the foot of a primitive Eocene primate *Notharctus*. *B*, the foot of a modern New World monkey *Cebus*. There has been a progressive development of the foot to a true plantigrade type in modern apes and man. (Redrawn from Gregory and Roigneau.)

and 3 are fused to form the elongate cannon bone, while 1 and 4 are reduced to splints associated with the fused second and third metacarpals. The foot has been tilted to the point that the animal is poised on the hoofs—the unguligrade pattern.

In the tapir this change has not progressed so far as it has in the horse. The third digit is the most prominent, but 2,4,5 are retained in the forefoot, while in the hind foot 2 and 4 remain, in addition to the third metacarpal. With these changes the wrist- and anklebones run almost in a vertical line with the metatarsals or metacarpals.

In primates evidence of tree ancestry persists in hand and foot (Figs. 94, 96, 97). Opposable thumb and great toe are common, and supination of the forearm is marked. In some South American spider monkeys, extreme length of fingers and a true prehensile tail may be associated with a vestigial thumb or with its absence.

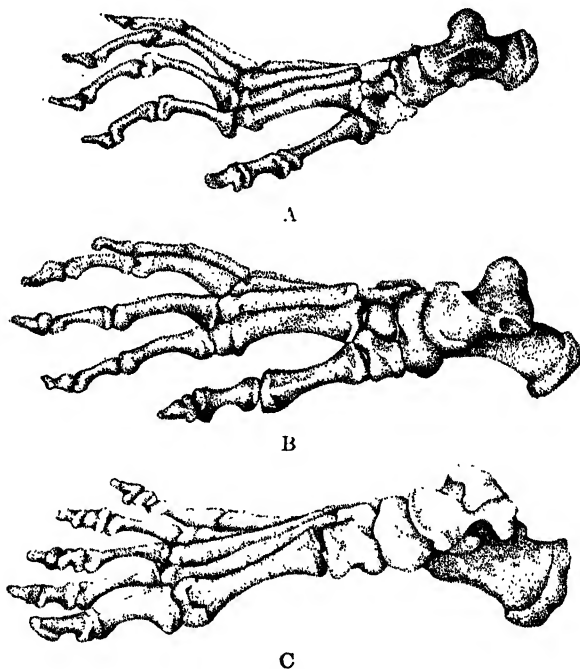


FIG. 97. A, foot of a present-day Old World monkey; B, the foot of the gorilla; C, foot of man. Note the shifting of the great toe from an opposing to a parallel position with the remaining digits and the progressive development of the heel. (Redrawn from Gregory and Roigneau.)

In man the axis of the hand is through the third digit; in the foot it is between the hallux and the second toe. The foot is modified for running, and associated with these changes the calcaneus and the arch are strengthened. The hallux has lost its opposability and becomes the most prominent toe. The generalized type of hand and foot, one of the priceless heritages of the mammals, together with their early arboreal habits, carried consequences which led to human development. The freeing of the hand, increased supination, the upright position of

the head, substitution of optic for olfactory sensation—all contributed to the fashioning of the creature we call man.

In specialized burrowing insectivores like the moles the humerus again is relatively short and develops heavy ridges associated with great power in the shoulder muscles. A large, sickle-like sesamoid bone increases the width of the shoveling hand. In another group, the golden mole of South Africa, a third forearm bone behind the ulna is a peculiar added feature associated with the digging habit. In the insectivores as a whole the hind limb is usually shortened.

THE SKULL

The term *head* has become proverbial in its connotation as a directing or focusing center for bodily activity. It is taken for granted that the animal must have a directing center, and yet we find, among invertebrate phyla, animals built upon a spherical or radial plan, in which the executive functions are not centered in a head. In a bilaterally symmetrical animal one end becomes dominant, and for a time it was believed that so-called axial gradients in the flatworms, for example, indicated that the degree of control diminishes from the cranial to the caudal ends. At the annelid and arthropod levels the head becomes the true directive center with a varying degree of specialized sensory development, although control through reflex nerve arcs permits a considerable degree of autonomy to other body parts. In advancing to higher vertebrate levels the body depends increasingly upon the activities of the head.

In this description we are concerned primarily with the protective and supporting skeletal structures that have evolved around the brain, the special sensory organs, and the structures for the apprehension and the preparation of food. These dual functions—one set related to protection and support of nervous tissue, the other to capture and intake of food—must be kept clearly in mind.

The skeletal case serving the first function is the *neurocranium*; the other, the jaws, are the *splanchnocranium* (Fig. 98A). These two parts, although different in origin, become closely associated and partly fused, as will be shown in the ensuing pages. The neurocranium results from the development of cartilaginous or bony plates and capsules; the splanchnocranium is a derivative of the visceral skeleton. Jointly, in their cartilaginous state, they are known as the *chondrocranium*.

Amphioxus. Amphioxus does not possess a head skeleton. The notochord which underlies the nerve cord extends to the rostrum and also supports the brain vesicle. The agnathic mouth has no skeletal

supports although the velum surrounding it is strengthened by delicate rods of procartilage.

In order to gain a clearer picture of the two parts of the chondrocranium, neurocranium and splanchnocranium will be dealt with separately.

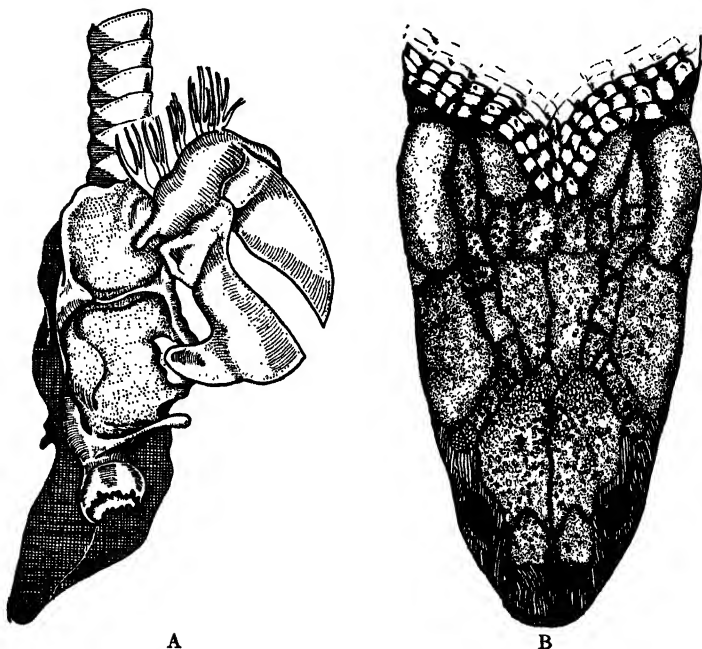


FIG. 98A. The elasmobranch skull. Skull and jaws are not fused. The latter articulate with the skull by an orbital process from the upper jaw and through the hyomandibular cartilage at the junction of upper and lower jaws.

FIG. 98B. The skull of *Polypterus*, a ganoid fish. Note the numerous dermal bones on the skull surface, which form an enveloping layer about a deeper cartilaginous layer corresponding to the skull of the elasmobranch.

Cyclostomes. In cyclostomes the cartilaginous chondrocranium includes the anterior part of the *notochord*, with which a pair of *parachordal plates*, one on each side, have become fused. This results in a *basal plate*, which is the floor of the brain case. Fused with posterior portions of the parachordal plates, a pair of *otic capsules* surround the inner ears. Extending anteriorly from the plates is another pair, the *trabeculae*, which at their anterior termination become fused with a

third cartilage, the *ethmoid*. Dorsal to the trabeculae and anterior to the brain a medial *nasal capsule* marks the original rostrum. In *Petromyzon*, perpendicular walls become associated with the basal plates and the otic capsules, and delimit the brain case laterally. The dorsal portion of the brain case at the level of the otic capsules is bridged over by a connective tissue tectum.

Two cartilaginous roof plates, somewhat lateral to the brain, one the posterior and the other the anterior, extend rostrally to the median nasal capsule.

The splanchnocranium in this agnathous group is a pair of *premandibular arches*, each with three vertical extensions to the floor of the brain case. The first of these extensions joins the anterior roof plate, the second with the posterior roof plate, the third with the nasal capsule. A median *glossal cartilage* supports the tongue, anterior to which is a semilunar *labial cartilage*. The remaining splanchnocranium is a series of *cartilaginous gill bars* associated with the vertebral column dorsally and fused into median, single, or paired bars ventrally.

Elasmobranchs. The elasmobranchs evolve further from the pattern first indicated in the cyclostomes. The parachordal plates fuse with the anterior end of the notochord; otic capsules fuse with these plates; trabeculae join the parachordals at the level of the hypophysis. These trabeculae unite anterior to a wide *hypophyseal window*. This is the so-called *platybasic skull*, i.e., with a wide fenestra between the trabeculae. The median ethmoid plate joins the anterior end of the trabeculae at the level of, and underneath, the olfactory lobes of the brain, while dorsally a pair of *alisphenoid cartilages* unite with the anterior margins of the otic capsules. These become part of the lateral wall of the skull case. Nasal capsules develop rostrally at the margins of the ethmoidal plates.

This growth results in a brain case expanded anteriorly by the nasal and posteriorly by the otic capsules. Between these expansions is the concave *orbit* for the eye. In front of the orbits a cartilaginous rostrum extends over the nasal capsules. The *sclerotic cartilages*, which are the outer wall of the eyeball, are analogous with the otic and nasal capsules, except that they do not fuse with the brain case, an apparent adaptation to movement of the eyeball.

Posteriorly the brain case expands by incorporation of three or four *occipital vertebrae* as part of the floor and the posterior wall. This becomes the occipital region of the skull. We thus recognize *occipital*, *otic*, *orbitotemporal-ethmoidal*, and *nasal* regions in this chondrocranium.

The roof of the brain becomes cartilaginous and in the adult elas-

mobranchs is completely so. The end result of these growth processes is a complete case with various openings for nerves and blood vessels. The spinal cord emerges through the greatest of these, the foramen magnum, in the occipital region. Fused with this case are the otic and the nasal capsules.

In elasmobranchs, with the exception of some of the rays, vertebral column and brain case are joined directly without intervention of a movable articulation. In the rays, paired condyles convert this joint to a diarthrosis.

The elasmobranch splanchnocranium has five to nine pairs of cartilaginous arches. The first two no longer support gills, while the remainder continue this function. The first arch, the *mandibular*, has become divided into two segments, the dorsal, or upper, jaw, and the ventral, or lower. The dorsal is called the *palatopterygoquadrate* cartilage, since it becomes so divided in amphibians and reptiles. The lower is *Meckel's cartilage*. Dorsal and ventral segments of one side fuse anteriorly with their fellows of the opposite side, completing the cartilaginous or bony margins of the mouth. Further, the lower jaw may be closed against the upper, transforming it into a biting mouth. The second, or *hyoid arch*, supports the mandibular. Its upper segment, the *hyomandibular cartilage*, attaches to the jaw at its articulation and also unites it with the skull; the lower portion of the hyoid is a tongue support. This type of jaw suspension through the hyomandibular cartilage is known as *hyostylic*.

The remaining arches are typically of four segments each. The dorsal segment, or *pharyngobranchial*, attaches to the vertebral column; the second, or *epibranchial*, is the lateral and dorsal gill support; the third, the *ceratobranchial*, forms the ventral and lateral part of the gill arch; the *hyobranchial*, a small ventral piece, attaches to the *copulas*. The latter are small longitudinal cartilages uniting the visceral basket along the midventral line. In some instances the copulas of the right and left sides do not fuse. The most posterior of these copulas is the *cardiobranchial* and may be considerably expanded. It lies approximately over the heart. Branchial rays and gill rakers, small, finger-like projections, are frequently associated with the arches.

The upper jaws are suspended in various ways. In elasmobranchs the hyomandibular connection with the jaw and skull has already been mentioned. Anteriorly, there is a second attachment in the region of the orbital process of the palatoquadrate and the skull in the *Chimaeras* and *lungfishes*. This type of suspension, in which jaw and brain case are directly connected, the *autostylic*, probably arose from an *amphi-*

stylic type found in primitive elasmobranchs in which otic, basal, and orbital processes, pushing dorsally from the upper margin of the palatoquadrate cartilage, made ligamentous connections with the chondrocranium, with additional support from the hyomandibular. In the autostylic type, the palatoquadrate is fused by its processes to the skull without any direct aid from the hyomandibular. Other types are the *holostylic*, in which the entire palatoquadrate is fused with the chondrocranium, found in holocephalan fishes, and *methystylic*, in which the palatoquadrate attaches to the otic capsule via the hyomandibular, found in teleostome fishes.

Small labial cartilages are frequently associated with the lateral margins of the jaws. These may be related to the premandibular cartilages of the cyclostomes, although at present their derivation has not been established.

It has been generally held by paleontologists until quite recently that the cartilaginous skull was ancestral to the bony type in which the dermal elements covered and frequently fused with the deeper cartilaginous portions.

Ganoid and Bony Fishes. Romer and others have pointed out the early appearance of bone in the fish ancestry. Romer suggests that, as a working hypothesis, the belief that early vertebrates were well ossified fits the known facts better than the possibility that they were cartilaginous, for the oldest known vertebrates were largely bony forms. He notes that cartilage is not present in connection with superficial dermal bones which show simple relationships and simple growth, but it occurs in internal bones of complicated structure in close relationship with other bones, blood vessels, and nerves. Since it has the power of expansion, in contrast to bone, which grows by superficial accretion, cartilage becomes the ideal material in embryonic growth, for it may later be replaced by bone. While it is probably as old as bone, he considers it an embryonic adaptation.

Regardless of the question of phylogenetic priority of bone or cartilage, the cranium is first laid down as cartilage in present-day vertebrates, and upon this foundation new elements are added from without. It is therefore spoken of as the *primordial cranium*. A new superimposed case becomes fused with this or may more or less completely replace it; this, the *dermatocranium*, arises in a way easily understood if one keeps in mind the great potentialities of the dermal skin layer. The problem is solved in a surprisingly simple manner. Scales which originally cover the head and jaws expand into a surface armor of many small plates, some of which may fuse, others drop out, resulting in a

few large, scale-like bones. These sink from the surface and cover and fuse with or replace the cartilage of the primordial cranium.

In primitive cartilaginous ganoid fishes (such as *Acipenser*, *Polyp-terus*) the primordial chondrocranium and the covering bones of dermal origin have not yet fused; in fact, the cartilaginous brain case is intact, and many of the overlying dermal bones retain a scale-like character (Fig. 98*B*). In bony ganoids, of which the bowfin *Amia* is representative, partial ossification of the chondrocranium extends from definite centers of bone formation. Such ossifications partly transform the original cartilaginous skull into a bony one, the latter made up of a number of ossified elements joined either by sutures or by fusions.

The fusion of the small, scale-like dermal bones in the ganoid and bony fishes results in larger elements which have been homologized with the bones of the tetrapod skull. Thus lacrimal, nasal, frontal, parietal, squamosal bones are identified on the dorsal and lateral aspects; parasphenoid and vomers in the roof of the mouth, premaxillae and maxillae in the upper jaw covering the palatoquadrate cartilage, while on the lower jaw the dentary overlies the lateral surface of Meckel's cartilage. Its medial surface is covered by splenial, angular, and surangular, with the articular at the point of articulation with the upper jaw. Medially over the roof of the mouth, pterygoids, entopterygoids, and palatines overlie the chondrocranium. Related to the otic capsule are sphenotic and pterotic bones that invade the cartilage of the capsule. The orbits are circumscribed by a ring of bones in which post- and preorbitals, post- and prefrontals, lacrimal and jugal are identified. Covering the operculum are preoperculars, suboperculars and interoperculars. These opercular additions disappear above the fishes. No part of the ancient neuro- and splanchnocranium is left untouched in this transformation.

Amphibia. Ossification of the skull is not yet complete in the Amphibia, and chondrocranium and dermal investing cranium may still be separated (Fig. 99*A*). The chief differences in the investing skeleton of Amphibia and bony fishes is the reduction in the number of bones, their disappearance from the surface, the dissociation of the hyomandibular from the jaw articulation and its conversion into the columella auris, and the appearance of a fenestra ovalis in the otic capsule. The latter, a window leading into the middle ear, is covered by a membrane, which is joined by the columella, derived from the hyomandibular. The amphibian brain case is small, and the upper jaw is fused with it.

Reptiles. The reptilian primary cranium is almost completely ossified (Fig. 99*B*). Some cartilage bones persist in the floor of the brain case,

e.g., ethmoids, and the otic capsule, while membrane bones form a complete second vault over the original brain case. Individual variations are great if one considers the divergence and range of the living and extinct reptilian species. A characteristic feature is the single occipital condyle, except in a few extinct *Cynognathus* forms. The quadrate is

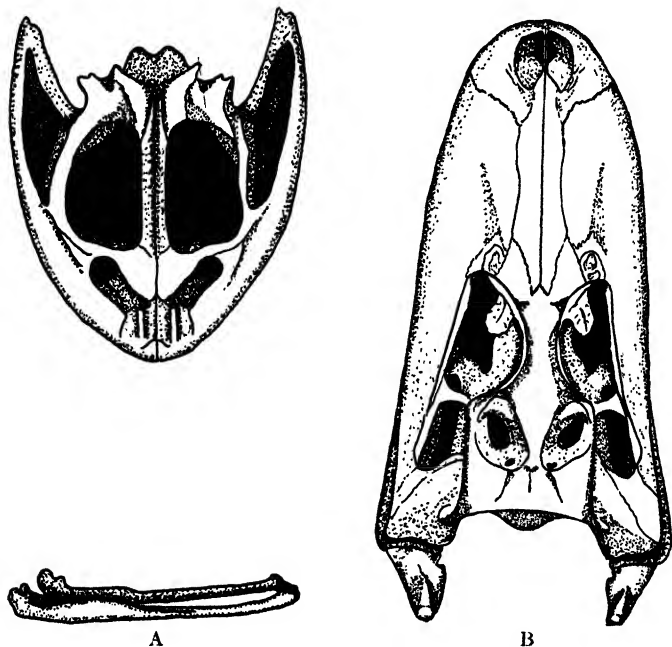


FIG. 99A. The amphibian skull. While both dermal bones and elements of cartilaginous origin are retained, there has been a great reduction in the number of skull bones.

FIG. 99B. The alligator skull. The neurocranium of the alligator constitutes but a small part of the skull. The upper jaws (splanchnocranium) fused with the neurocranium constitute its larger part.

fused with the squamosal bone except in the snakes, where it is movable, much as it is in birds, where through its muscle, the quadratoorbital, it elevates the upper jaw. The choanae have moved back because of wide palatine processes on the maxillary bones. Teeth are general in the group save in the turtles. They appear on premaxillae and on the dentary and in some species on the palatines. The temporal region, subject to great variations, shows various types of fenestration. These

fenestrations have been used in tracing phylogenetic relationships. In one of these, the *diapsid* type, an upper arch, consisting of squamosal and postfrontal, and a lower zygomatic arch, the quadratojugal and jugal, lie in the temporal region; in another type, the *anapsid*, found in the turtles, the entire temporal region is completely roofed without fenestration or arching; in a third, the *synapsid*, only a dorsal temporal fossa occurs. Its ventral border is a bony arch comprising a process from the squamosal and the body of the jugal bone. The term *synapsid* indicates that a fossa has been closed by coalescence of two arches, which, however, is not the case.

In the upper jaw, premaxillary and maxillary, with which are associated vomers, palatines, pterygoids, and quadratojugals, all representing dermal additions, are the functional parts. The quadrate, a remnant of the original palatoquadrate cartilage, is retained between the squamosal portion of the temporal and the quadratojugal bone. In the lower jaw the dentary, of dermal origin, bears teeth and constitutes its outer two-thirds. The splenial is on the medial margin, the articular at the point of meeting with the upper jaw, the angular at the outer angle below the surangular, and the coronoid, a new element, placed between the angular and surangular. The hyomandibular, converted to the columella auris, extends between fenestra ovalis and the eardrum. The columella has a stapedial and an extrastapedial part; the first fits into the fenestra ovalis by an expanded base; the second, small and rod-like, extends to the eardrum. An inconspicuous valve-like opening to the outer ear, in the alligator and some lizards, is easily overlooked; in others the ear membrane may face directly on the skull.

Birds. The neuro- and splanchnocranium of birds are greatly modified in comparison with those of their reptilian predecessors, chiefly by the presence of very large eyes, often larger than the brain, and by the elongate beak (Fig. 100). The enlarged eyes result in a narrow inter-orbital septum by pushing together the orbitosphenoids; the ethmoids are prevented from participation in the cranial floor, and the temporal fossae are reduced.

Ossification of the neurocranium begins early, and the bones which replace it may be fused in individuals at the age of a few months. Cartilages of the primary chondrocranium become ossified and become the basioccipitals, exoccipitals, and supraoccipitals; the otic, opisthotic, epiotic, and prootic bones; the basisphenoids, aliorbitosphenoids, and presphenoids and mesethmoid. Dermal bones covering the neurocranium are parietal, frontal, nasal, prefrontal, squamosal, and zygomatic. Associated with the jaws and roof of the mouth are the maxillary, pre-

maxillary, vomer, and parasphenoid; covering the palatoquadrate cartilage are the quadrate, pterygoid, palatine, and quadratojugal bones. The sclerotic support of the eyeball may be ossified and results in a telescope-like, bony protrusion around the optic cavity, usually of a number of pieces.

The premaxillary, much larger than the maxillary, constitutes the anterior part of the upper beak, while its margins are the maxillary. The premaxilla has three processes, palatine, maxillary, and frontal, directed posteriorly, each named after the bone it joins. The maxillary bone has a palatine process, which may be fused with its neighbor medially to form a hard palate. The nasals are well developed, each with a premaxillary, maxillary, and frontal process, which together surround the external nasal apertures. The vomers, usually fused, may join the parasphenoid in the roof of the mouth. The parasphenoid underneath the floor of the brain case develops from three primordia, an anterior rostral one usually joined with the vomer, and two posterior ones, commonly fused as the basitemporal (basipterygoid), particularly well developed in the pheasants. The rod-like pterygoids join the quadrates posteriorly and the palatines anteriorly. The palatines lie between the pterygoid and the premaxillary. The quadrate, as the name implies, is roughly squared and unites with the skull secondarily. It has an otic process, joined to the capsule, an orbital process articulated with the quadratojugal, and it also articulates with the pterygoid bone. The quadratojugal contributes the posterior part of the zygomatic arch and articulates with the zygomatic process of the maxillary or may join the zygomatic bone when that is present.

A peculiarity common to many birds and to some reptiles (*Squamata*) is the ability to raise the upper beak or upper jaw (Fig. 101). This is possible because of a free quadrate which articulates with the quadrato-

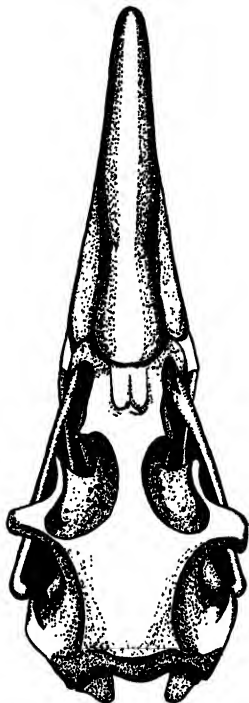


FIG. 100. The bird skull (albatross). The brain case is expanded in comparison with the reptilian skull. Accommodation for large eyes is achieved by compressing the region between.

jugal and the pterygopalatine arch. One of the ventral processes of the quadrate, it will be recalled, articulates with the quadratojugal, another with the pterygoid. The orbital process of the quadrate has the protractor quadrati muscle attached, and on its contraction the quadrate bone is pulled anteriorly, as well as rotated. This in turn pushes the quadratojugal and the pterygopalatine mechanism forward and raises the beak. The nasals and the temporal processes of the premaxillary are sufficiently flexible to respond to this pressure.

In the lower jaw the articular is ossified and joins the quadratojugal at the articulation. The dentary is prominent on the outer surface, a splenial on the medial surface, and an angular at the outer angle, the latter with a posterior process giving attachment to the depressor man-

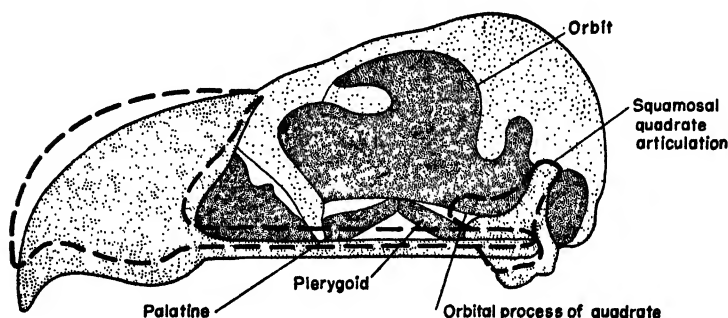


FIG. 101. Movement of maxilla in the bird. The maxilla in certain birds may be elevated by muscle pull on the quadrate bone. Heavy dotted line shows range of movement. (Redrawn from Ihle and Versluys.)

dibulae muscle. The hyomandibular of the original second branchial arch becomes the columella auris. The third arch furnishes a copula as a tongue support, the latter with paraglossal extensions which may circle the skull and terminate in the right dorsum of the upper beak. The bones are pneumatic. Associated with the nasal choanae are maxillary, premaxillary, mesethmoid, nasal, and prefrontal sinuses, while opening into the tympanic cavity are the sinuses of the skull capsule.

In a survey of the skull and the jaws, two primary principles appear operative. One is the principle of continuity, which apparently dictates that, when changes occur from order to order or from class to class, they must be built on existing structures. A second is that which permits, during the evolution of species, the transposing and transforming of parts not originally associated. Thus neurocranium and splanchnocra-

nium, the latter derived from the first pair of branchial arches, approximate each other and function together, or chondrocranium and dermal bones, the latter derived from scales, join to form the skull above the ganoid level. Ear bones fashioned from remnants of the mandibular and hyoidean arches, by transposition and remodeling, make new associations and assume unique functions in the middle and inner ear.

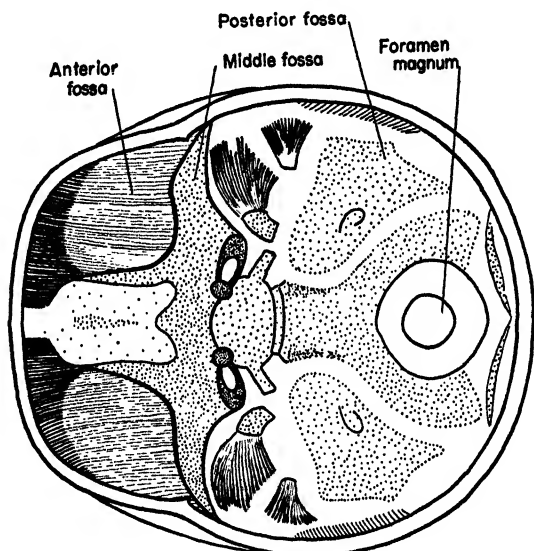


FIG. 102. Internal view of human skull. The human skull exhibits an anterior, middle, and posterior fossa. Stippled basic-occipital and sphenoidal elements constituting posterior and middle fossae are of cartilaginous origin. Lined anterior fossa representing floor of frontal bone is of dermal origin. (Redrawn from Cunningham.)

Changes from class to class are gradual, in spite of the discontinuous *sprungweise* nature of mutations. Transitions may be followed in the skull that have been interpreted as bridging the gap between elasmobranchs and ganoids, between ganoids and bony fishes, between the crossopterygian fishes and the Stegocephalia, between these and amphibians and reptiles, and between the latter and the birds on the one hand and the mammals on the other. Where such evolutionary transitions are verified, it becomes evident that a constant simplification of existing parts and a reduction of the number of elements in the system have taken place. Thus, when ossification of the skull begins, it does

not stop at the ganoid level but continues through teleost, amphibian, reptilian, mammalian levels, just as the heart does not stop at the single atrium-ventricle stage but evolves into an efficient mechanism with a right and a left atrioventricular system. There is an apparent logical sequence in the manner in which protoplasm develops and changes; it springs from universal cause-and-effect relationships operative in creating a structure or in developing a function.

Mammals. The mammalian chondrocranium shows some divergence from that of the elasmobranchs. The skull is *tropybasic*, which means

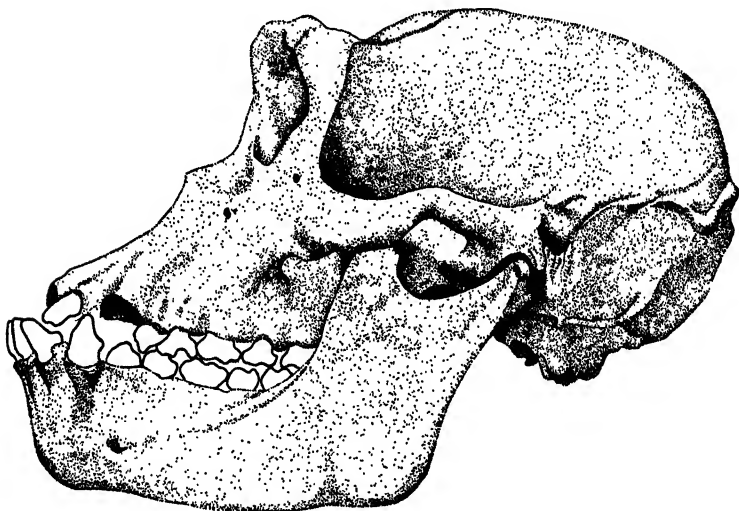


FIG. 103A. Lateral view of chimpanzee skull. Note heavy eyebrow ridges prognathous jaws, and lack of frontal development.

that in their growth the bodies of the trabeculae fuse and leave only a relatively small foramen for the hypophysis. In the *platybasic* skull, on the other hand, the anterior ends of the trabeculae are fused, leaving a wide hypophyseal fenestra between their medial margins. A chondrocranial roof is absent, although both a posterior and an anterior membranous tectum join the lateral and the posterior walls of the brain case.

With the introduction of lung breathing in land animals, a condition forecast in both crossopterygian and dipnoan fishes, the nasal sac ultimately is divided into a ventral air passage and a dorsal olfactory organ. The epithelium of the latter may become extensive through the appear-

ance of cartilaginous turbinals associated with the ethmoid plate and the nasal septum. The auditory capsule, too, is expanded by the emergence of a cochlea from the lagena of the vestibule and by the older pars vestibularis.

Trabeculae develop as small cartilaginous islands in the hypophyseal region and not as plates continuous with the parachordals, as in the



FIG. 103B. Anterior view of chimpanzee skull.

elasmobranchs. Extracranial space between the palatoquadrate and the chondrocranial wall is incorporated in the brain cavity, and with this increase the otic capsules are pushed farther into the floor of the case. The palatoquadrate cartilage by its otic process attaches to the auditory capsule and by its basilar extension joins the basipterygoid.

The dermal skull becomes fused with the ossified cartilages of the chondrocranium (Figs. 102 to 104). The roofing bones are entirely dermal, while those of the floor and the lateral walls are enchondral, or of cartilaginous derivation. Palatal processes of the maxillaries and

palatine bones together form a hard palate, shifting the internal nares far back into the roof of the mouth. Pterygoids of dermal origin are pushed posteriorly, where they become the lateral borders of the choanae. The hooks (hamuli), fused with the pterygoids, in contrast to the pterygoids themselves are of cartilaginous origin. Double occipital condyles have replaced the single tripartite reptilian condyle, apparently by the dropping out of the segment contributed by the basioccipital. A single petrosal bone, fused from epiotic, opisthotic, and prootic elements,

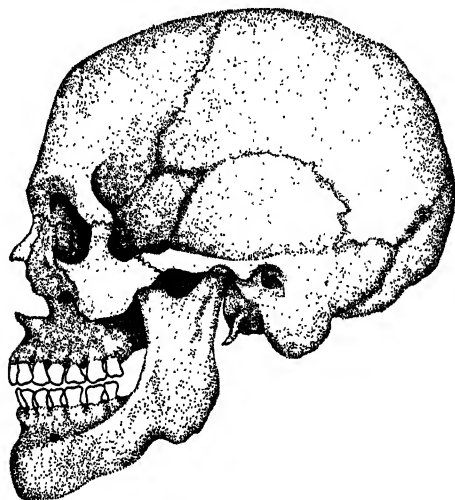


FIG. 104A. Lateral view of human skull. Note relatively small jaws, reduction of eyebrow ridges, and prominent frontal development in comparison with Fig. 103.

houses the membranous ear labyrinth. Ossification of the basal plate and incorporation of the lateral alisphenoids with it result in a bone that serves as part of the brain floor—its lateral and anterior walls—and in that expansion contribute to the orbital wall (basisphenoid, presphenoid, orbitosphenoid, alisphenoid). The pituitary gland has lost its fenestra and lies in the small excavated sella turcica on the floor of the basisphenoid. The original parasphenoid which pushed forward in the midline of the skull floor appears to have been lost, with the exception of its anterior end, which presumably has produced a new vomer; while the reptilian prevomers are fused with the premaxillae as their palatal processes. A single mesethmoid cribriform plate completes the anterior brain-case wall.

The lower jaw, reduced to a single dentary bone, articulates directly with the squamosal, which is also dermal and has become part of the skull. In the upper jaw, premaxillary and maxillary bones have replaced the palatoquadrate and carry the teeth. The hyomandibular has long since been incorporated into the middle ear as the columella auris (stapes). The articular end of Meckel's cartilage, no longer employed as an articulating element with the upper jaw, has likewise been

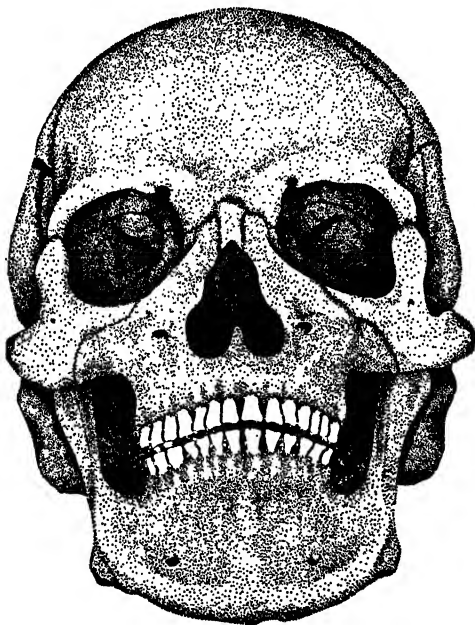


FIG. 104B. Anterior view of the human skull.

taken into the middle ear as the incus, while the quadrate cartilage of the original upper jaw, discarded as an articulating bone, becomes the malleus. These changes, which have here been touched on only most superficially, give evidence of the restless potentialities in the skeleton, a division of the body which from an uncritical viewpoint may appear static or dead.

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CHAPTER 5

THE MUSCULATURE

MOVEMENT

Movement is characteristic of all protoplasm. It may change the relations of various parts within the living cell or animal, or it may change the position of the cell or animal in space. Internal and external movements follow from the fact that animals and cells are dynamic organizations, and their vital attributes are associated with such changes.

Typical intracellular movement involves protoplasmic streaming. This results from the various physical and chemical forces acting upon the solutions and formed bodies within. Associated with such purely internal movements are the segregation and removal of secreted substances.

Internal movement may result from changed tension or changed permeability of the cell wall or membrane, producing turgor. Imbibition as well as loss of fluids is responsible for this movement, more commonly associated with plant cells.

A primitive type of external cellular movement is ameboid movement. Like turgor, ameboid movement results from modifications of the cell membrane and involves transformation from a gel-like to a more liquid or soluble state. With the yielding of the cell membrane, temporary protrusions called pseudopodia are produced which are perhaps the first definitive locomotor mechanisms.

In the protozoan world two types of permanent locomotor mechanisms, cilia and flagella, commonly effect external movement; these types identify two great classes, the Ciliata and Flagellata. In the single-celled Protozoa these whip-like processes propel the organism from place to place. In Metazoa, cilia and less frequently flagella are incorporated in epithelial structures and transport particles or fluids along various internal channels. Ameboid movement also persists as in leukocytes and in neural processes in embryonic stages. Epithelial tissues such as the mucous membrane of the pharynx and bronchi and the testicular ducts and oviducts are lined with these ciliated cells. Flagellate cells in the epithelium of some glandular ducts and in certain serous membranes are also retained as the locomotor mechanism of the male germ cells in the chordates.

The cilium and flagellum consist of a firm axial filament surrounded by a fluid contractile sheath. The filament appears to originate in a granule beneath the cell membrane and terminates beyond the sheath as a free, whip-like structure. Movement is directed and coordinated by the basal granule. Filament and sheath are activated by rapid production of an acid, followed by oxidation. This is comparable with the action of lactic acid on the myofibril in the smooth muscle, which is also followed by oxidation.

MUSCLES

In *Hydra*, one of the coelenterates, external as well as internal movement is effected by musculoepithelial cells that probably represent the

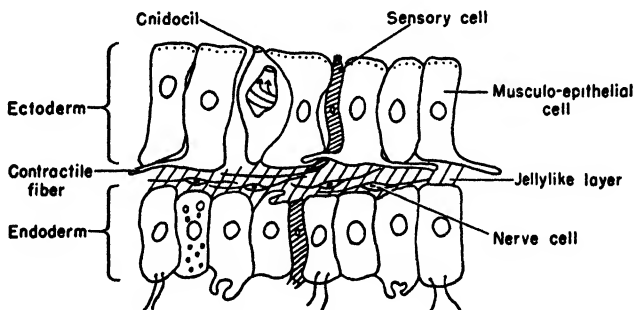


FIG. 105. Musculoepithelial cells—*Hydra*. The contractile cells in the ectoderm of *Hydra* are derived from the epithelial cells. They send processes to the underlying tissues.

first specialized contractile cells (Fig. 105). In annelids a large part of the body is smooth muscle. Arranged in circular and longitudinal bands, it produces the typical movement in this group.

In chordates the following three types of muscles are developed: (1) smooth (involuntary), the least specialized, in walls of blood vessels, digestive tract, bronchi, etc. (Fig. 106A), (2) cardiac, confined to the heart, retaining some features of smooth muscle but structurally modified (Fig. 106B), and (3) striated, forming a multinucleate syncytium, comprising the voluntary muscles of the body (Fig. 107).

Smooth Muscle. Smooth muscles form a wall of considerable thickness for the stomach, urinary bladder, and uterus and are present in the walls of blood vessels of the trachea and bronchi, in the ducts of many glands, and in the intestinal tract (Fig. 108). Almost universally

distributed, they regulate the mechanics of such varied activities as gland secretion, peristalsis, bladder constriction, changes in the size of blood vessels, and movements of the iris.

Smooth muscles are usually excited by impulses from the autonomic nervous system and also by the chemical agents, known as hormones, secreted by the endocrine glands. They respond to many hormones such as adrenalin, sympathin, pitressin, pitocin, and acetylcholine. This response may be contraction or relaxation after contraction. Upon stimulation they respond much more slowly than striated muscle, requiring 3 sec. to 3 min. to contract, while striated muscles respond

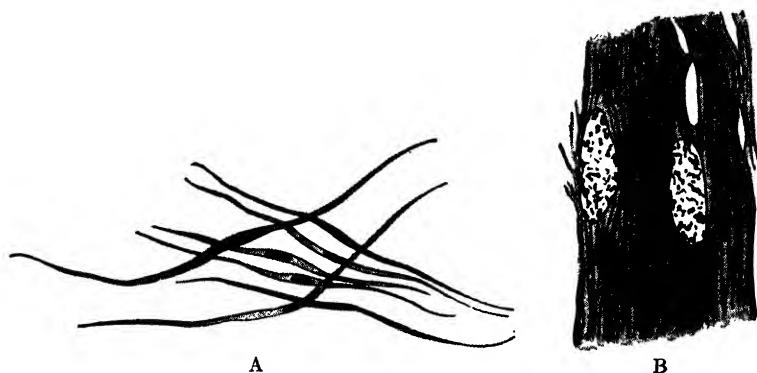
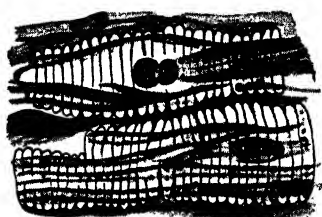


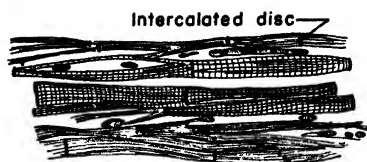
FIG. 106. A, smooth muscle fibers. The cells are characterized by their spindle shapes and their relative shortness in comparison with striated muscle fibers. B, detail of smooth muscle cell. The nuclei are centrally placed, and elongate fibrils extend through the cells. (*Redrawn from Maximow and Bloom.*)

within 1 sec. or less. Experimentally, smooth muscles may be excited to rhythmic contraction by a continuous stretching force, such as excess fluid in the urinary bladder. Normally they exhibit marked tonus, enabling them to resist overstretching. The diameters of digestive tube, blood vessels, and ducts are restricted, for example, within normal limits by this action. When overconstriction occurs in arterial walls, owing to a pathologic condition, hypertension may result. Smooth muscle generally is involuntary, although in the urinary bladder some voluntary control is possible.

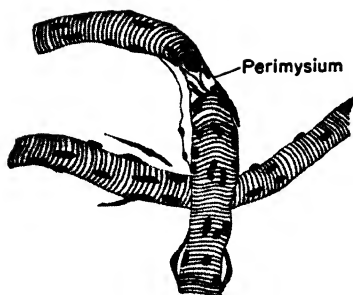
The muscles are short, spindle-shaped cells varying from 0.2 to 0.5 mm. in length and 0.006 mm. thick, each with a single centrally placed nucleus. The body of the cell has minute myofibrils surrounded by fluid sarcoplasm. The latter may contain glycogen granules, mitochondria,



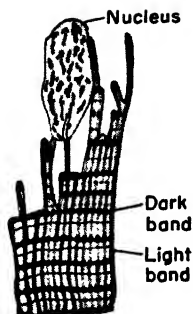
A



B



C



D

FIG. 107. A, cardiac muscle fibers reveal cross striations under magnification. B, intercalated discs cross bundles of cardiac muscle fibers at irregular intervals. C, striated muscle fibers reveal characteristic cross markings that traverse bundles of fibers. Nuclei are peripheral; delicate perimysium covers the fibers. D, photomicrograph of striated muscle. (A, B, and C are redrawn from Maximow and Bloom. D, courtesy of the General Biological Supply House, Chicago.)

and a Golgi network. Smooth muscles are not attached to the skeleton but are variously arranged in the connective tissues of the organs they serve and may be either isolated or grouped in bundles. Where they are abundant, they are closely surrounded by elastic fibers, which in turn are associated with loose connective tissue, permitting the transmission of contractions from the muscle to the surrounding tissue network. The arrangement of smooth muscles in circular or longitudinal bands around a duct or vessel regulates either the constriction or the shortening of the lumen.

Striated Muscle. Striated muscles, also called skeletal or voluntary, although probably derived from smooth, differ markedly from them in structure, function, and distribution. According to their function they may be *spindle-shaped*, or fusi-form, *e.g.*, the biceps brachii; *bipinnate*, or feather-shaped, the muscle fibers radiating diagonally from the tendon, *e.g.*, the interossei; *unipinnate*, in which the tendon is attached at the side of the muscle fibers, *e.g.*, flexor pollicis longus; *flat* sheets, in which the muscle originates and inserts by wide aponeurotic tendons, *e.g.*, the abdominal muscles.

Striated muscles make up the major portion of the locomotor system in the chordate body. Collectively they are the great system for transporting the mass of the body from place to place, or they change the position of one part of the body with relation to the remainder. They have reached a stage of efficiency in many land animals where they can

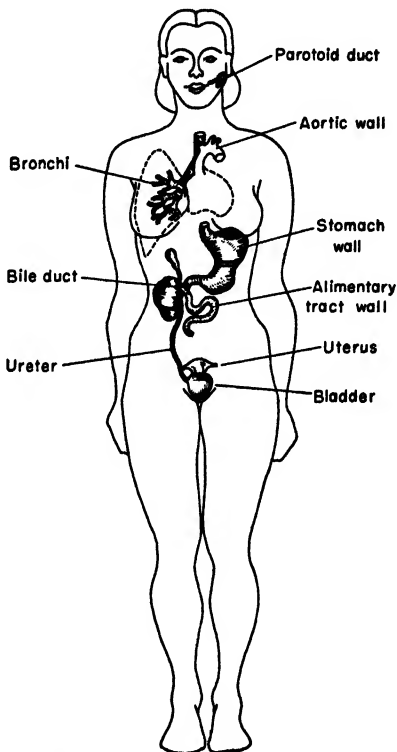


FIG. 108. Schematic view of smooth muscle distribution. The entire arterial and venous channels, exclusive of the capillaries, are also supplied with smooth muscles.

convey the body at speeds up to 60 miles per hour for short distances. It must be remembered that they can act in this manner only with the cooperation of skeletal, nervous, and circulatory systems and that they are influenced greatly by glandular secretions as well.

Striated muscles consist of muscle fibers, which are individual cells or structural units, forming delicate strands up to 40 mm. in length with a thickness of 0.01 mm. Frequently a number of nuclei appear in a single fiber, giving rise to a multinucleate cell, or syncytium. The ends of a fiber may be tapered, serrated, or branched; the individual fiber is covered by a thin transparent membrane, the sarcolemma, absent in smooth muscle. Within this membrane is the fluid sarcoplasm, in which delicate myofibrils may extend throughout the length of the cell. Sarcoplasm contains glycogen and pigment as well as fat droplets and is usually most plentiful around the nuclei. Microscopic striations pass across the myofibrils to the surrounding sarcolemma. Each myofibril is made up of alternating light and dark sections so arranged that respective sections in adjacent fibers correspond. This results in the striated appearance of the muscle and is responsible for its name.

Striated muscle fibers are arranged in primary bundles separated by a thin membrane, the *endomysium*. Primary bundles combine to form secondary ones, and the latter form tertiary aggregates, bound together by elastic fibers and surrounded by a sheath of connective tissue, the *perimysium*. At their termini an *epimysium* encloses the perimysium and passes directly into the tendinous portions of the muscle.

Cardiac Muscle. Cardiac muscle is confined to the heart. In back-boned animals it combines into bands of fibers differing in some respects from smooth and striated muscle. In contrast to striated muscle, the nuclei are centrally placed. Free muscle endings do not occur since the fibers are arranged in a continuous anastomosing network. The anastomosing fibers assure a continuous nervous impulse or wave over the entire heart, once the stimulus is received. Clear areas about the nuclei are filled with sarcoplasm containing fat droplets, mitochondria, and pigment granules. A thin sarcolemma covers the muscle fiber. *Intercalated discs* occur at regular intervals across the fibers. Since the fibers pass uninterruptedly through the discs, the latter are probably not cell boundaries, as was formerly thought. Dark and light sections alternate in the myofibrils to form typical striations, and the fibers are associated in bundles as in striated muscles.

A peculiar modification of cardiac muscle, the *Purkinje fibers* in the interventricular septum probably constitute the conducting system of the heart, since they convey and distribute the nervous impulse. They must not be confused with the innervation supplied by the vagus nerve

and the sympathetic nervous system. Cardiac muscle requires $\frac{3}{10}$ to 2 sec. to respond to stimulation. It is involuntary but responds rapidly to emotional excitement.

The heart, which has taken on the specialized function of pumping the blood stream to the tissues and organs, shows a variable development in the different vertebrate classes as well as within the individual classes or species. Its size is indicative of the blood volume and of the activity of the animal.

The following tabulation of a few representative heart weights and body weights associated with them indicates the great range in size of this specialized muscle tissue:

TABLE 3. HEART-BODY WEIGHT RATIOS

Animal	Body weight, kg.	Heart weight, gm.	Ratio
Elasmobranch fishes:			
Electric ray (<i>Torpedo torpedo</i>)	0.345	0.22	1:1,568
Sting ray (<i>Dasyatis sabina</i>)	2.675	6.83	1:391
Sand shark (<i>Carcharias littoralis</i>)	35.38	41.60	1:850
Bony fishes:			
Perch (<i>Perca flavescens</i>)	0.192	0.44	1:436
Codfish (<i>Gadus callarias</i>)	2.52	3.90	1:645
Jewfish (<i>Promicrops itaiara</i>)	32.89	49.23	1:666
Amphibia:			
Bullfrog (<i>Rana catesbiana</i>)	0.339	1.37	1:247
Gila monster (<i>Heloderma suspectum</i>)	0.514	4.17	1:120
Reptiles:			
Black snake (<i>Coluber constrictor</i>)	0.590	6.08	1:97
Turtle (<i>Clemmys guttatus</i>)	2.16	7.05	1:306
Green turtle (<i>Chelonia mydas</i>)	68.04	180	1:307
Birds:			
Crow (<i>Corvus brachyrhynchos</i>)	0.337	3.2	1:105
Tawny eagle (<i>Aquila rapax rapax</i>)	2.62	18.54	1:141
Fowl, white Orpington (<i>Gallus domesticus</i>)	2.20	8.78	1:251
Man-of-war bird (<i>Fregata aquila</i>)	1.40	16.59	1:85
Ostrich (<i>Struthio camelus massaicus</i>)	123	1,205	1:1,020
Carnivores:			
Arctic weasel (<i>Mustela arcticus</i>)	0.169	2.83	1:59
Cat, domestic (<i>Felis domesticus</i>)	0.576	3.00	1:192
Genet cat (<i>Genetta tigrina suahelica</i>)	1.52	8.46	1:180
Wildcat (<i>Felis ocreata</i>)	2.70	15.86	1:170
Dog, police (<i>Canis familiaris</i>)	38.42	261	1:142
Lion, (<i>Felis leo</i>)	191	1,017	1:186

TABLE 3. HEART-BODY WEIGHT RATIOS (Continued)

Animal	Body weight, kg.	Heart weight, gm.	Ratio
Rodent:			
Guinea pig (<i>Cavia cutleri</i>).....	0.351	1.72	1:202
Porcupine (<i>Erethizon dorsatus</i>).....	2.80	19.75	1:142
Richardson's ground squirrel (<i>Citellus paryii paryii</i>).....	0.878	5.85	1:150
Capybara (<i>Hydrochoerus isthmus</i>)....	14.96	55.06	1:269
Ungulate:			
Dik-dik (<i>Rhynchotragus dirki</i>).....	4.57	36.08	1:126
Giraffe (<i>Giraffa camelopardalis</i>).....	1,220	4,990	1:245
Stallion, equipoise (<i>Equus caballus</i>)..	521	4,455	1:117
Rhinoceros (<i>Rhinoceros bicornis</i>)....	764	5,400	1:141
Cetacea:			
Porpoise (<i>Phocaena phocaena</i>).....	142	738	1:193
White whale (<i>Delphinapterus leucas</i>)..	303	1,722	1:175
Finback whale (<i>Balaenopterus physalus</i>)	59,394 (130,946 lb.)	382,000 (842 lb.)	1:155
Primates:			
Lemur (<i>Galago senegalensis</i>).....	0.200	1.138	1:145
Macaque (<i>Macacus rhesus</i>).....	3.63	12.20	1:299
Red spider (<i>Ateles geoffroyi</i>).....	2.81	14.52	1:193
Chimpanzee (<i>Troglodytes niger</i>).....	52	250	1:204
Chimpanzee (<i>Troglodytes niger</i>).....	44	219	1:209
Human:			
Male Chinese, adult.....	84	555	1:152
Maya Quiche, age 25.....	42	220	1:191
White male, age 25.....	78	331	1:233
White female, age 44.....	43	220	1:195

The last column indicates the ratio of body weight to heart weight, in other words, the number of units of body weight corresponding to each heart unit. These values carry significant implications from which many of the energy characteristics of the animals may be deduced. They show among other things the way in which this great bundle of cardiac tissue has become adapted to the various activities of different animals or, conversely, how heart development has permitted adaptations in energy release. If one had only these data, one might draw significant conclusions about the energy characteristics of the animals involved.

THE MECHANICS OF MUSCLE ACTION

Levers. Acting together, striated muscle and skeleton form a mechanical system for the performance of work (Fig. 109). Such work, as

indicated, may move the body as a whole or change the position of one part with reference to another. The various types of attachments between muscles and skeletal parts result in different lever systems.

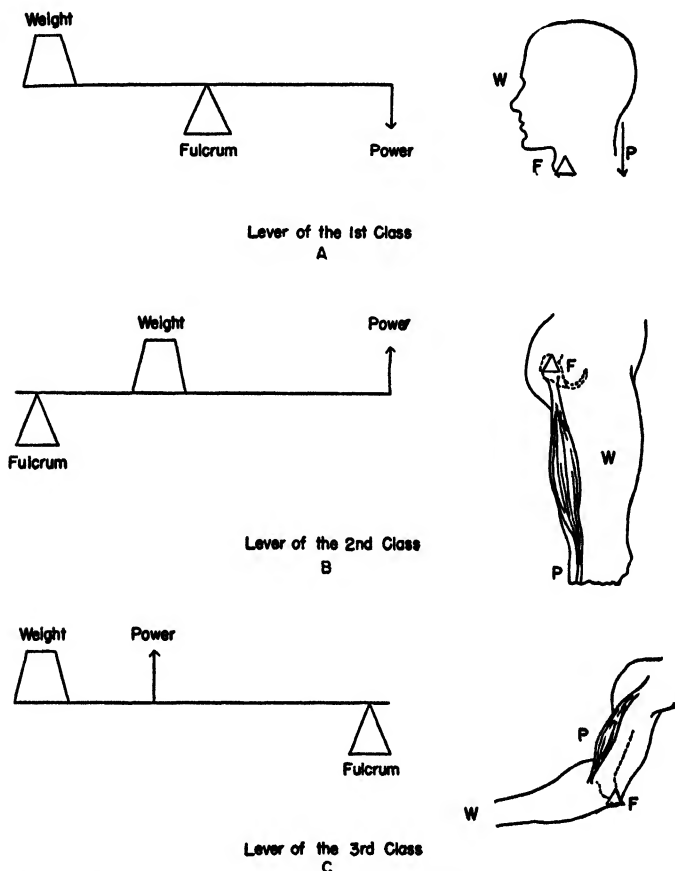


FIG. 109. Types of levers. (B, lever of second class, not represented in intact body.)

Three such classes of levers are recognized, depending upon the inter-relations of power, weight, and fulcrum. In a lever of the first class the weight is at one end of the lever arm, the power is applied at the other, and the fulcrum is between the two. A seesaw is an example of this type. In man, the head supported on the vertebral column with its

associated musculature is a lever of the first class. If the head is to be flexed, the weight may be considered concentrated behind the axis and the power is applied anteriorly. Power and weight are reversed when the head is thrown back or extended.

In levers of the second class the weight lies between the fulcrum and the force of the lever arm. This type does not occur in the human and

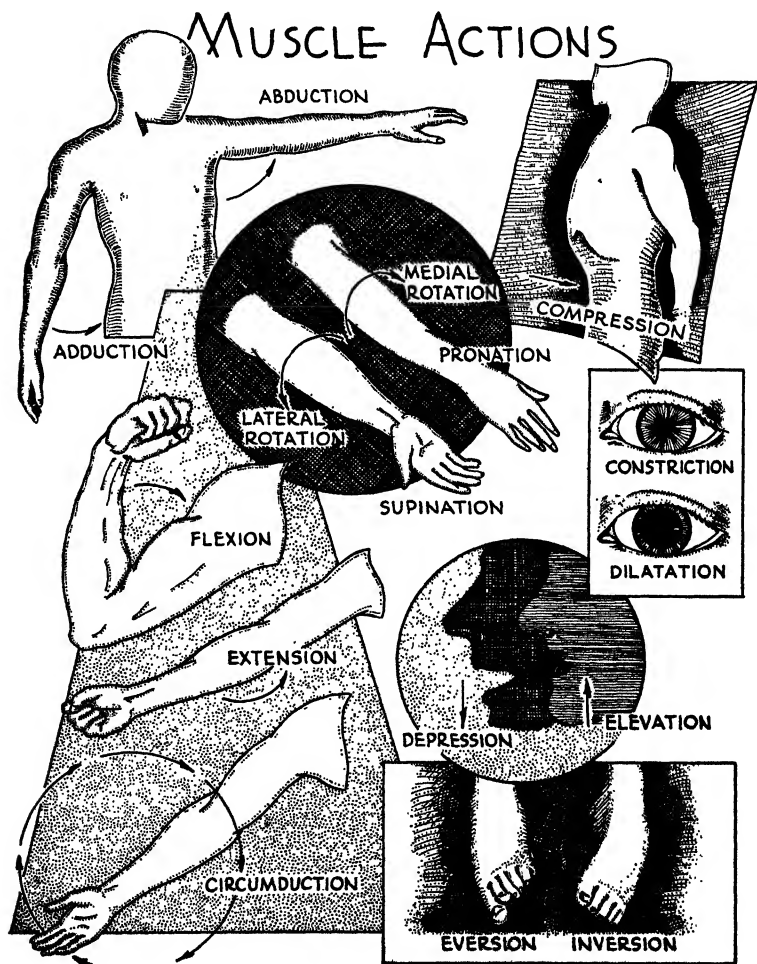


FIG. 110. Types of muscle action.

the animal body. In a lever of the third class the power is applied between the weight and the fulcrum. This is the most common type of leverage found in animals. The biceps brachii and the radius and ulna to which it is attached form such a system. The weight is represented by the hand and the forearm, the fulcrum is at the elbow articulation, and the power is applied at the radial tubercle about $1\frac{1}{2}$ in. below the fulcrum and at the *lacertus fibrosus*.

In addition to their action as parts of lever systems, muscles exert direct pulls to move body parts. Thus the epaxial muscles of the fish and the *rectus abdominis* muscle of man approximate body parts without employing levers. In such a system no mechanical advantage is gained, because a force equal to the sum of the weight and the resistance of the moved part must be employed. Gravity plays a role in movement, particularly in such activities as walking, stooping, depressing the lower jaw, or lowering the arms.

Levers as they are employed in the body generally give the advantage of movement through large arcs. This does not necessarily imply a mechanical advantage, since the energy expended for a given movement may be great. An arm or leg may be carried through a considerable distance at the periphery by means of relatively small contractions at the proximal end. The point of skeletal attachment determines the type of advantage to be gained.

TYPES OF MOVEMENT

A number of distinctive movements occur in the animal body (Fig. 110). Usually each type of movement has its opposite, or antagonist, since muscles act only by contraction and to return a part to its original position requires a set of opposing muscles. Muscles rarely act singly. Many actions are synergistic, the result of a number of muscles working together. Such action does not contradict the principle of antagonism. Further, in most movements a prime mover is recognized. This is aided or checked by other muscles acting in a varying capacity. The following muscle actions are recognized:

TABLE 4. TYPES OF MOVEMENT

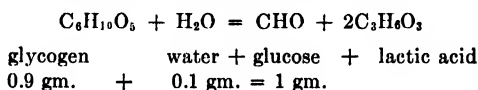
<i>Type of movement</i>	<i>Definition</i>
Flexion.....	Decrease of angle between adjacent parts separated by an articulation (in the normal range of movement)
Extension.....	Increase of the angle between adjacent parts separated by an articulation (in the normal range of movement)

TABLE 4. TYPES OF MOVEMENTS (*Continued*)

<i>Type of movement</i>	<i>Definition</i>
Abduction or protraction.....	Movement away from the central axis of the body, as in raising the arm horizontally from the side of the body or in thrusting forward the lower jaw
Adduction or retraction.....	Movement toward the central axis of the body, as in lowering the arm from a horizontal position to the side of the body or in pulling back the lower jaw
Elevation.....	Lifting a part, as in raising the lower jaw
Depression.....	Lowering a part, as in opening the mouth by action on the lower jaw
Pronation.....	Turning the forearm so that the palm faces downward
Supination.....	Turning the forearm so that the palm faces upward
Medial rotation.....	Turning the entire appendage on its long axis so that the thumb or great toe describes an arc directed medially
Lateral rotation.....	Turning entire appendage on its long axis so that the thumb or great toe describes an arc directed laterally
Circumduction.....	Movement of appendage, head, or trunk on a pivot at the proximal end so that the distal end describes a circle
Compression.....	Reduction of the size of a cavity, as in expiration of air from the lungs
Constriction.....	Reduction in size of an opening, or lumen, <i>e.g.</i> , mouth and anal sphincter; reduction in circumference of blood vessels by smooth muscles
Inversion.....	Movement of the foot so that the sole faces medially
Eversion.....	Movement of the foot so that the sole faces laterally

THE NATURE OF MUSCLE CONTRACTION

Muscle contraction involves expenditure of energy. This is derived from glycogen stored in the muscle or in the liver and making up as much as 0.9 per cent of the muscle weight or up to 27 per cent of the liver weight in the rabbit on a carbohydrate diet. It is the primary source of energy for muscle contraction, resulting in work and heat production. The glycogen combines with water to form glucose, which in a series of reactions is converted into lactic acid. According to Plunkett the reaction may be summarized as follows:



Plunkett has calculated the energy released by 1 gm. of lactic acid as follows:

TABLE 5. ENERGY RELEASED IN MUSCLE ACTION

	<i>Energy</i>	<i>Calories</i>
Total energy liberated by muscle (in absence of oxygen) per gram of lactic acid.....		0.370
Potential energy of 0.9 gm. of glycogen.....	3.836	
Potential energy of 1 gm. of lactic acid.....	3.601	
Difference equals energy liberated by conversion of glycogen to lactic acid....		{ 0.235 }
Energy liberated by neutralization of 1 gm. of lactic acid by protein.....		{ 0.135 }
Total.....	0.370	0.370

In other words this reaction yields 0.370 calorie per 0.9 gm. of glycogen. According to one theory of muscle contraction, glycogen is concentrated at the surface of the myofibrils, and lactic acid is formed at this site. The myofibrils consist of proteins in an ionized state, primarily as anions. With production of lactic acid the protein ions are neutralized. This reaction enables the cohesive forces acting on the molecules of the myofibrils to pull them together and shorten the fibrils. With diffusion of the lactic acid into the surrounding sarcoplasm the protein molecules again become negatively charged. The anions again repel each other and counteract the cohesive action of surface tension, thus relaxing the fibril.

With accumulation of lactic acid, the muscle becomes fatigued unless supplied with sufficient oxygen. In the presence of oxygen, approxi-

mately one-fifth of the lactic acid is oxidized, with the liberation of energy as external work or as heat within the muscle, while the remaining four-fifths is reconverted into glycogen.

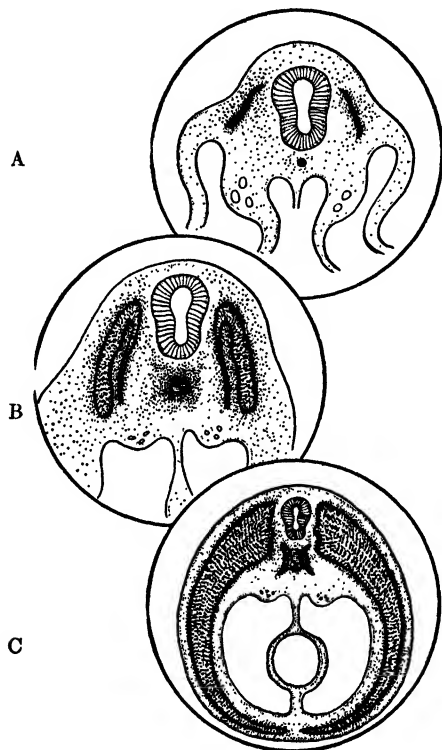


FIG. 111. Origin of myotome from epimere. *A*, epimere after differentiation of mesomere and neuromere; *B*, epimere differentiating into sclerotome, dermotome, and myotome; *C*, myotome and lateral muscle plate have completed the thoracic and abdominal muscle wall.

ORIGIN OF MUSCLES

Muscles are derived from mesoderm, the middle germ layer of all triploblastic embryos (Fig. 111). In vertebrates, with the exception of the cyclostomes, the mesoderm first forms a solid cellular outgrowth between ectoderm and endoderm, beginning on each side of the neural tube and extending laterally and ventrally. During growth it is differ-

entiated into an upper *epimere*, a middle *mesomere*, and a ventral *hypomere*. The hypomere divides tangentially into an outer somatic and an inner splanchnic layer. The inner, or splanchnic, layer surrounds the *archenteron*, or primitive gut, and forms the smooth muscle and connective tissue of its wall. The outer, or somatic, layer furnishes the lining of the body cavity. The space between the two divisions is the body cavity, or *celom*.

Beginning at the head, the epimere is divided into vertical segments separated by partitions called *myosepta*. These divisions do not extend into the mesomere and hypomere. Specializations in the epimere form the sclerotome, which provides the cells for the vertebral column; the dermatome, which gives rise to the deep layer of the skin; and the myotome, from which the somatic muscles of the trunk and appendages develop. The myotomes grow ventrally and push between the integument and the somatic mesoderm. In fishes and amphibians a *horizontal skeletogenous septum* of connective tissue separates the sheet formed by the downward growth of the myotomes into a dorsal *epaxial* and a ventrolateral *hypaxial* portion. In reptiles, birds, and mammals the epaxial part evolves into the *transversospinalis muscles* of the back and the hypaxial into the *abdominal muscles* and their derivatives. These two divisions mark the origin of the somatic muscles of the entire body. The appendicular muscles are derived secondarily from the myotomes, as will be shown.

TRUNK MUSCLES

Amphioxus and Cyclostomes. Although a horizontal skeletogenous septum is absent, the general arrangement of the trunk muscles of *Amphioxus* and cyclostomes resembles that of fishes (Fig. 16). Over the dorsum of *Amphioxus* the epaxial muscles show a primitive segmental arrangement, and along the ventral portion of the trunk in the pharyngeal region a sheet of muscle corresponding roughly to the hypaxial musculature of fishes occurs. Cyclostomes have a similar distribution of trunk muscles. In the gill region the myotomes are interrupted, and dorsal and ventral somatic muscle segments are distinguishable. In the head region, three pairs of myotomic segments give rise to the six pairs of eye muscles.

Fishes. In fishes the epaxial myotomes have angular "zigzag" margins, producing typical herringbone stripes in the muscular sheet (Fig. 112). This folding permits the myosepta to attach to the spines and bodies of several vertebrae. On the ventral side, where the abdominal musculature is differentiated into elongate sheets, the folding is less

pronounced In teleost fishes a ventral abdominal muscle splits from the hypaxial sheet. This "red muscle," superficial to the hypaxial muscles, extends from the shoulder girdle to the anal aperture. Ventral to the gills the hypaxial muscles are united with the coracoid bar and with the hyoid and mandibular arches. They split into coracobranchial, coracohyoid, and coracomandibular muscles. These hypaxial muscles are not to be confused with branchiomic, or visceral, muscles, to be described later, which eventually displace the hypaxial in part and lie external to them. While reduced dorsally over the gills, the epaxial muscles continue to the skull. As in cyclostomes, the three pairs of head myotomes give rise to the six pairs of eye muscles.

Amphibians. The transition from aquatic to land life in amphibians is associated with numerous changes in the somatic muscles (Fig. 113A

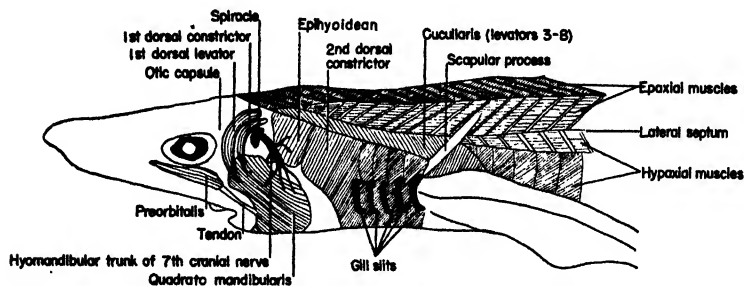


FIG. 112. Epaxial and hypaxial muscles of the dogfish. Note the retention of zigzag myotomes separated by myocommata and their interruptions at the gill openings.

and B). Epaxial muscles are less prominent generally than in fishes, since locomotion is no longer the dominant function of the trunk. The vertebral column becomes a true articulating mechanism with joint processes at the bases of the laminae in addition to the joints at the centra. Some of the deep fibers of the epaxial muscle mass, now called the *dorsalis trunci*, become attached to the transverse and articular processes and spines of the vertebrae. This marks the appearance of definite spinal muscles which move individual vertebrae. Likewise a movable head on the vertebral column occurs for the first time in amphibians. The anterior end of the *dorsalis trunci* divides into two extensor muscles, which attach to the head. With these changes the segmental myosepta of the back muscles lose their original skeletal attachments and are gradually replaced by fascia and aponeuroses.

This changes the original short myotomic back muscles into bands of varying length with tendinous rather than with myoseptal attachments.

The hypaxial musculature of amphibians is also more specialized than

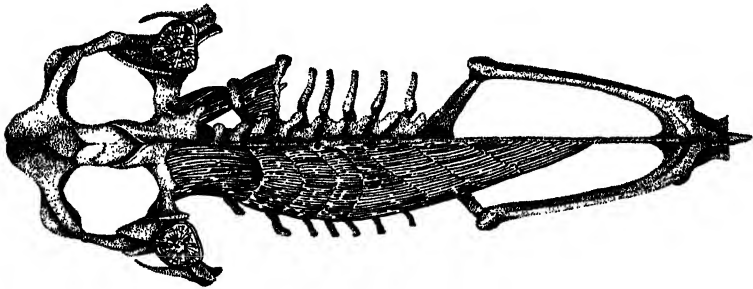


FIG. 113A. Epaxial muscles of the frog. The primitive myotomic pattern is undergoing modification to form a dorsal muscle mass; occipital muscles that move the head are developed. (Redrawn from Evans.)

that of the fishes (Fig. 114). The muscle primordium just below the lateral septum is the origin of *external* and *internal oblique abdominal* muscle sheets. Right and left sheets extend ventrally and are joined in

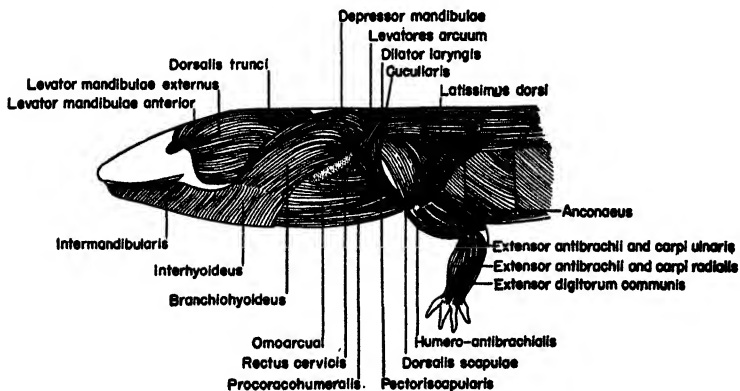


FIG. 113B. Lateral view of muscles of *Necturus*. Land life has correlated with it a high degree of specialization of limb muscles.

the midline by fascia, the *linea alba*. Fibers of the external oblique muscle extend diagonally downward toward the midline, while those of the internal oblique extend at right angles to the external. Both

muscles, by tangential splitting, subdivide into superficial and deep layers. From the inner surface of the internal oblique muscle, migrating cells form the deepest abdominal layer, the transverse abdominis muscle, with fibers running at right angles to the long body axis.

On the underside of the body, lateral to the midline, a fourth pair of hypaxial muscles, the *recti abdomini*, extend from the pelvic girdle to the head. These are also derived from the hypaxial sheet.

Reptiles. In reptiles, birds, and mammals, the epaxial trunk musculature is divided into three columns variously developed according to the habitat and manner of life peculiar to its own particular class.

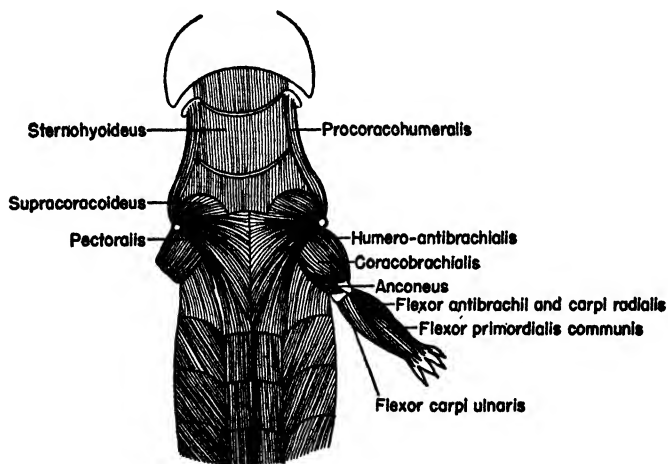


FIG. 114. Ventral muscles of lizard. Differentiation includes the neck muscles employed in swallowing, as well as the limb muscles.

The three columns are the *iliocostalis*, the *longissimus*, and the *transversospinalis*. The last named and most medial of the three covers the laminae of the vertebrae. Lateral to it the *longissimus* covers the transverse processes of the vertebrae, while the *iliocostalis*, the most lateral, extends from the ilium to the head at the level of the angles of the ribs. In creeping reptiles, the *iliocostalis* is the best developed of the three and moves the column from side to side. With the backbone, aided by specialized abdominal scales, this epaxial muscle is the chief locomotor mechanism of creeping forms. The deeper portion of the *transversospinalis* system retains much of its original segmental character. It consists of short muscles which originate on a specific part of a

vertebra and insert on a corresponding part of an adjacent vertebra. Thus there are developed *interspinalis* muscles between adjacent vertebral spines, *intertransverse* between transverse processes, and *interarticular* between articular processes. The *levator costarum*, another group of deep muscles, pass from the proximal ends of the ribs to the transverse processes of the vertebrae above. These, while epaxial in position, are hypaxial in origin.

Reptiles, like amphibians, have external and internal oblique abdominal muscles, both hypaxial, with both superficial and deep divisions. Ribs, greatly reduced or absent in amphibians, are outstanding in reptiles. In addition to those articulating with vertebrae, others, known as abdominal ribs, or *gastralia*, and completely independent of the vertebrae, appear in the Crocodilia and in some lizards (Fig. 80). The rectus abdominis muscle, which unites the pelvis with the sternum, becomes segmental in the region of the gastralia, since the ribs intercept its superficial layer. Associated with the ribs attached to the backbone are *external* and *internal intercostal muscles*. These are hypaxial muscles derived from the external and internal abdominal oblique muscles, respectively.

Birds. The highly specialized vertebral column and pelvis of birds, together with the great development of flight muscles, have made possible a reduction of the three epaxial muscular columns, except in the region of neck and tail. In the neck the transversospinalis fibers appear as two extensors of the neck, a *biventer cervicis* and a *complexus muscle*. In the tail the epaxial muscles move the coccyx and tail feathers.

Hypaxial muscles are the *anterior rectus*, a deep muscle joining the head and neck; the *longus capitis* and *longus colli*, flexors of the head and neck; the *external* and *internal abdominal oblique muscles*; the *rectus abdominis* and the *transverse abdominis*, compressors of the abdomen. *Intercostal muscles* are poorly developed.

Mammals. Since the mammalian body depends increasingly on legs, in comparison with many reptiles, the trunk muscles of mammals assume new functions (Fig. 115). The viscera are suspended from the vertebral column, which has become adapted to support this weight. Individual vertebrae are closely joined by ligaments and by short dorsal muscles associated with the transverse and articular processes, and with spines of the column. Firm attachments also exist between the vertebral column and pelvis. Suspension of a movable head at the end of a long neck has produced changes in the vertebral column and modifications of the neck ligaments and muscles. In the trunk the thoracic musculature becomes adapted to the respiratory movements of the ribs.

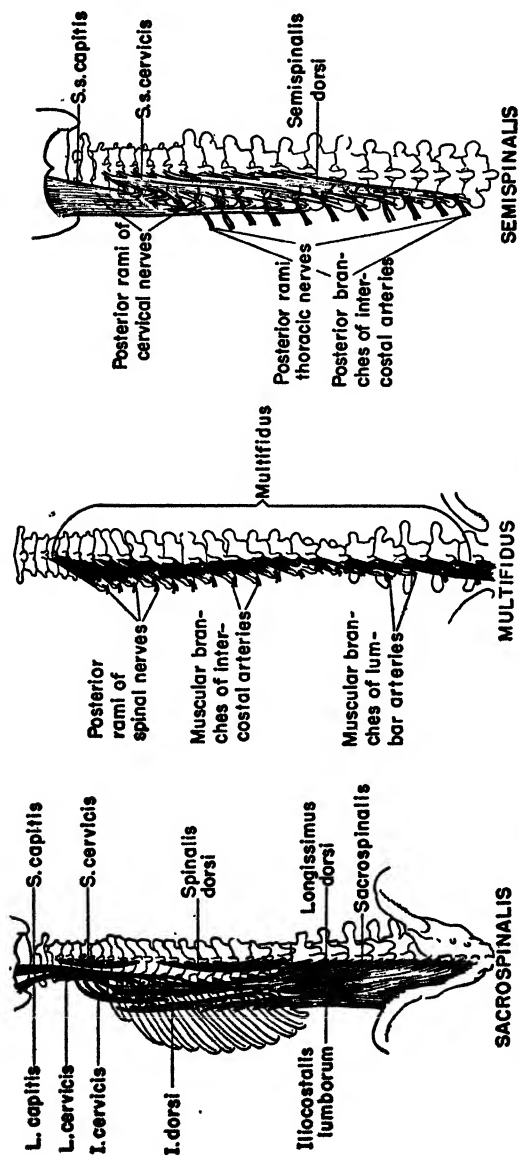


Fig. 115. Back muscles of man. The original metameric pattern is overshadowed by the long, strap-like muscles. (Courtesy of Lea and Febiger.)

Although a lateral septum is absent in mammals, trunk muscles are divided into dorsal epaxial and ventral hypaxial groups. Collectively, dorsal muscles are extensors and ventral muscles are flexors of the column, although other actions may result when these muscles act singly or unilaterally. The dorsal group includes *splenius cervicis* and *capitis*; and *sacrospinalis*, which separates into three columns, a lateral *iliocostalis*, intermediate *longissimus*, and medial *spinalis*. A fourth muscle associated with this group is the *semispinalis*, medial to the *spinalis*. Short muscles intimately connected with the column are the *multifidus*, *interspinalis*, *rotatores*, *intertransversarii*, and *levator costarum*.

Of the above group, *splenius*, *longissimus*, *spinalis*, and *semispinalis* have *capitis* divisions which extend from the neck to the head. Acting upon the head, also, are the major and minor *rectus* muscles, each with an anterior, lateral, and posterior division, and two pairs of oblique *capitis* muscles, with superior and inferior divisions. On the dorsal aspect of the neck the *splenius*, *iliocostalis*, *longissimus*, *spinalis*, and *semispinalis* have cervical divisions uniting the neck with the thorax. The last four muscles are also represented by dorsal divisions over the thorax. In the lumbar region the *iliocostalis lumborum* and the *quadratus lumborum* unite the vertebral column with the pelvis.

Table 6 will help to visualize the divisions in these mammalian epaxial muscles.

TABLE 6. DIVISIONS OF THE SACROSPINALIS MUSCLE

	Iliocostalis	Longissimus	Spinalis	Semispinalis	Quadratus lumborum
Head.....	capitis	capitis	capitis	
Neck.....	cervicis	cervicis	cervicis	cervicis	
Thorax.....	dorsi	dorsi	dorsi	dorsi	
Lumbar region	lumborum	lumbar only

Caudal epaxial muscles are greatly reduced in those mammals in which the tail is vestigial or absent. When present, they are extensors or abductors of the tail. In man the coccygial muscles are remnants of this group.

The mammalian hypaxial musculature, like the epaxial, is highly differentiated. Beginning on the ventral side of the head and connecting the occipital bone with the upper end of the vertebral column are the short *rectus capitis anterior*, the *lateralis*, and the *longus capitis*. On the ventral and lateral sides of the neck are the *longus colli* and three pairs of *scalene* muscles, the latter connecting the upper ribs with the

neck. An infrahyoid group, an extension of the rectus abdominis, unites the sternum with the hyoid arch. The muscles of this group are the paired sternohyoids, sternothyroids, and thyrohyoids. On the ventral side of the thorax are external and internal intercostals and the transverse thoracic muscles. These ventral muscles are extensions of the rectus abdominis, external and internal abdominal oblique, and transverse abdominis muscles. In tailed mammals specialized hypaxial caudal muscles act as flexors of the tail.

VISCERAL, OR BRANCHIOMERIC, MUSCLES

The epimeres do not account for all voluntary muscles. In the gill region of the Ichthyopsida, or fish-like vertebrates, muscles appear which cannot be traced back to epaxial or hypaxial groups (Fig. 116 *E*). These are visceral, or branchiomic, muscles that originate from splanchnic mesoderm, the latter, as already mentioned, forming the inner layer of the hypomere and surrounding the primitive intestine. In the pharyngeal region elements from this splanchnic mesoderm move forward to the gill arches and develop as specialized constrictors and levators of the gills and jaws.

Amphioxus and Cyclostomes. In *Amphioxus*, branchiomic muscles retain their primitive smooth character. In the cyclostomes they have evolved into gill constrictors and are covered by the somatic muscles. In this class, as in the remaining vertebrates, they are striated muscles.

Fishes. In fishes the branchiomic muscles lie superficial to the somatic muscles of the pharyngeal region and evolve into three specialized groups, each supplied by a cranial nerve. The first group, the most cephalad, is associated with the fifth cranial (trigeminal) nerve and with the jaws. It includes the levator of the maxilla, which attaches the upper jaw to the neurocranium; the intermandibularis, later the hylohyoid, between the rami of the lower jaw, and the adductor mandibularis, between the angles of the lower jaw and the skull. The last also elevates the lower jaw. In certain elasmobranch fishes preorbital muscles may split from the branchiomic sheet supplied by the trigeminal nerve. They attach to the anterior floor of the orbit and insert in common with the adductor mandibularis.

The second muscle group, associated with the seventh cranial (facial) nerve and with the hyoid arch in fishes, consists of a superficial facial constrictor lying just posterior to the intermandibularis. In mammals it becomes the platysmal sheet, covering the anterior surface of the neck and the face, evolving into the muscles of expression.

The third group comprises the superficial neck and facial constrictors

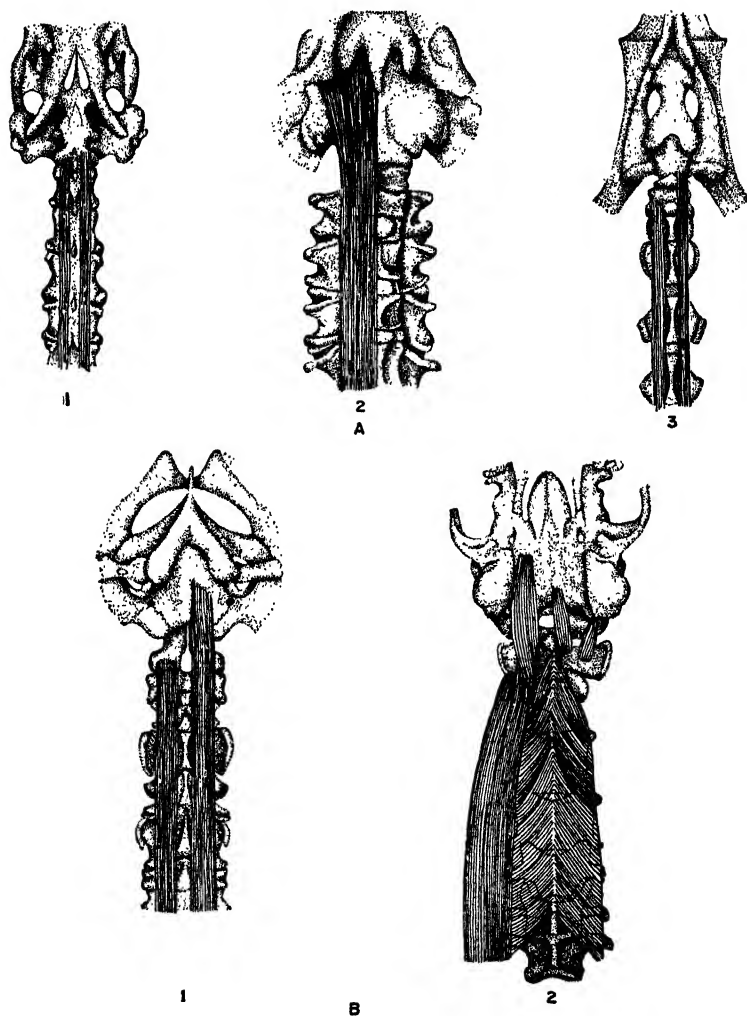


FIG. 116. Subvertebral muscles of various animals. A, 1, *Sphenodon*; 2, *Diadectes*; 3, *Iguana*. B, 1, *Cynodont*; 2, *Felis*. (Redrawn from *Evans*.)

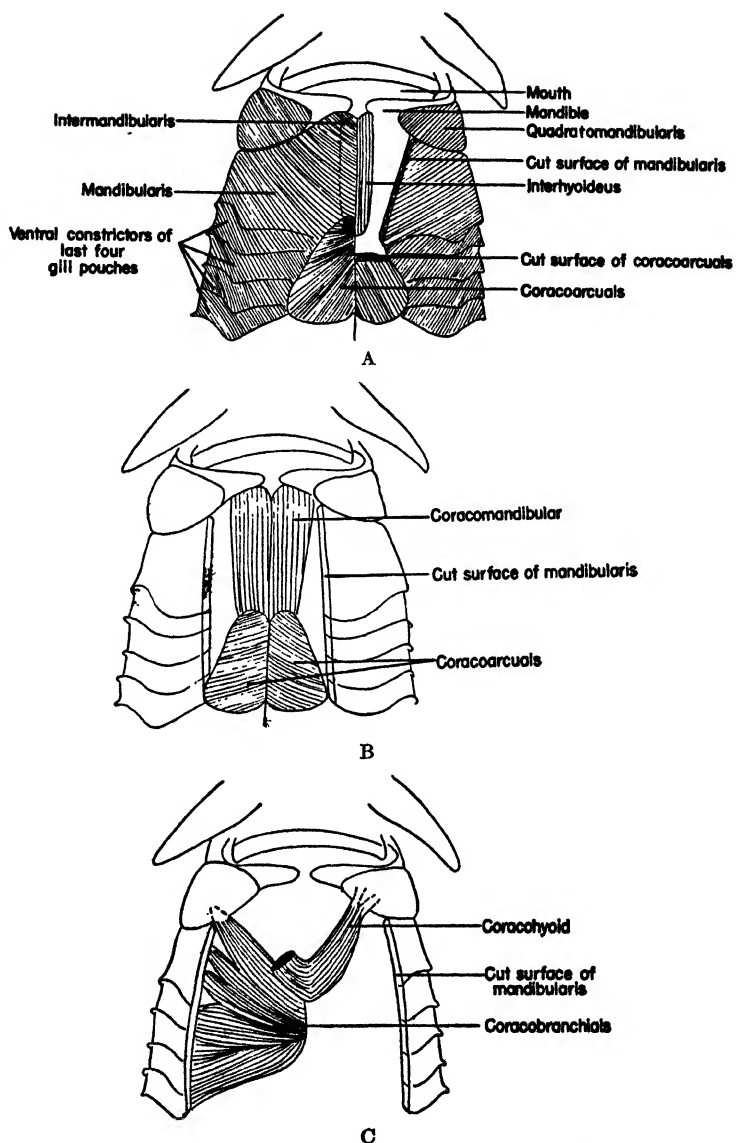


FIG. 117. *A*, brachiomeric muscles, superficial, of dogfish; *B*, deep brachiomeric muscles of dogfish; *C*, brachiomeric muscles associated with gills in the dogfish. (Redrawn from Ihle.)

and in land animals the intrinsic muscles of the larynx, the pharyngeal constrictors, the trapezius, and the sternocleidomastoid. It is supplied by the vagus nerve and in mammals in part by the accessory.

Amphibians. The branchiomeric muscles of amphibians are a series of dorsal and ventral constrictors, levatores of gills, dorsal to the constrictors, and interarcual muscles, uniting the upper ends of the gill arches in those amphibians which retain gills (Fig. 117A, B, C). In amphibians that undergo metamorphosis these muscles, although remaining attached to the modified gill arches, are converted into pharyngeal constrictors and levatores (Fig. 118A, B).

Reptiles. The reptilian branchiomeric muscles are represented by those attached to the jaws, by those associated with the hyoid arch, and by two muscles connected with the scapula and clavicle (Fig. 119A, B).

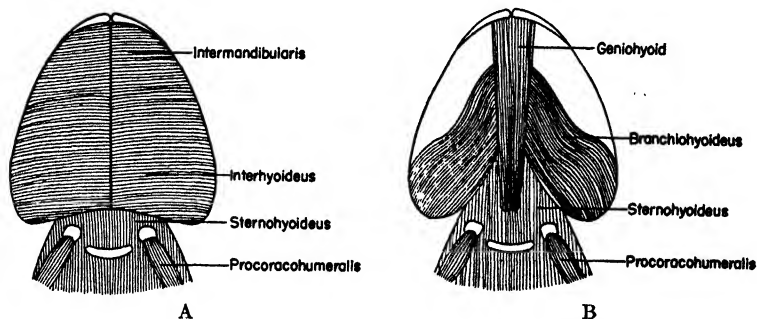


FIG. 118. A, superficial branchiomeric muscles in Amphibia; B, deep branchiomeric muscle in Amphibia. (Redrawn from Ihle.)

The first are supplied by the fifth cranial nerve. They include paired external and internal pterygoids, from the ramus of the lower jaw to the pterygoid bone of the skull; the adductor mandibulae, from the lateral surface of the skull to the angle of the jaw that in mammals separates into paired temporals and masseters. Between the rami of the lower jaw lies a third muscle of mastication, the intermandibularis, a continuation of the constrictor sheet that covers the anterior surface of the neck. Associated with upper jaw and skull, a levator maxillae superioris unites the palatoquadrate bone with the skull. In the orbit it becomes the levator bulbi, which causes protrusion of the eye, while another division, the depressor palpebrae inferior, retracts the lower eyelid. The depressor mandibulae, also, of this group joins the skull with the posterior surface of the lower jaw. This muscle disappears in mammals.

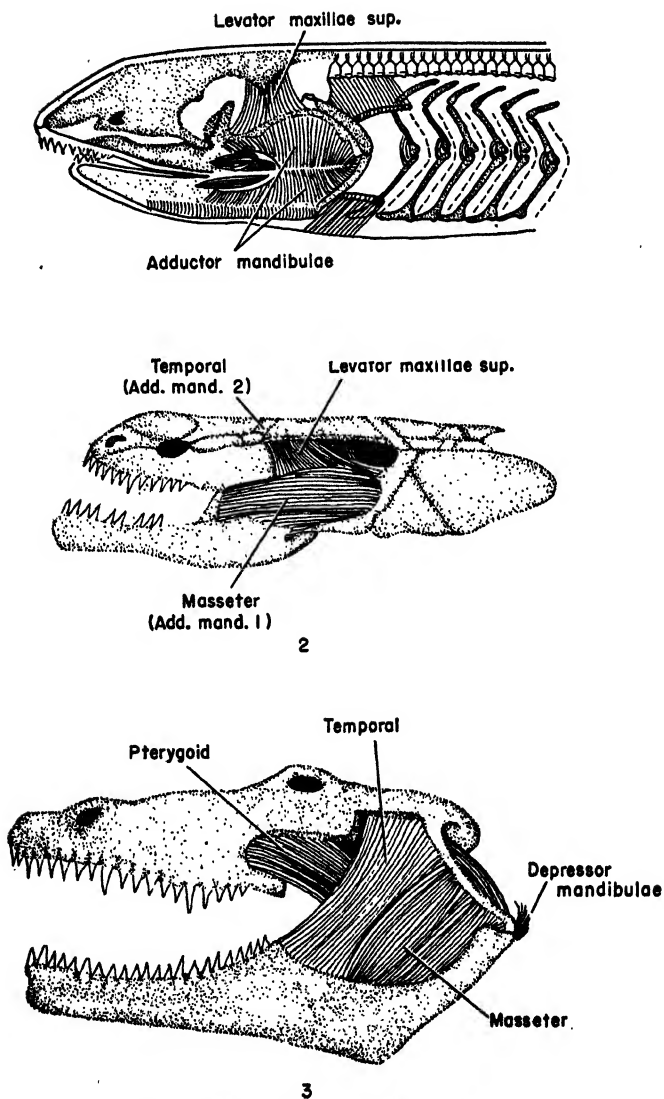


FIG. 119A. Evolution of jaw muscles. 1, shark; 2, lobe-finned ganoid; 3, primitive amphibian. (Redrawn from Gregory and Roigneau.)

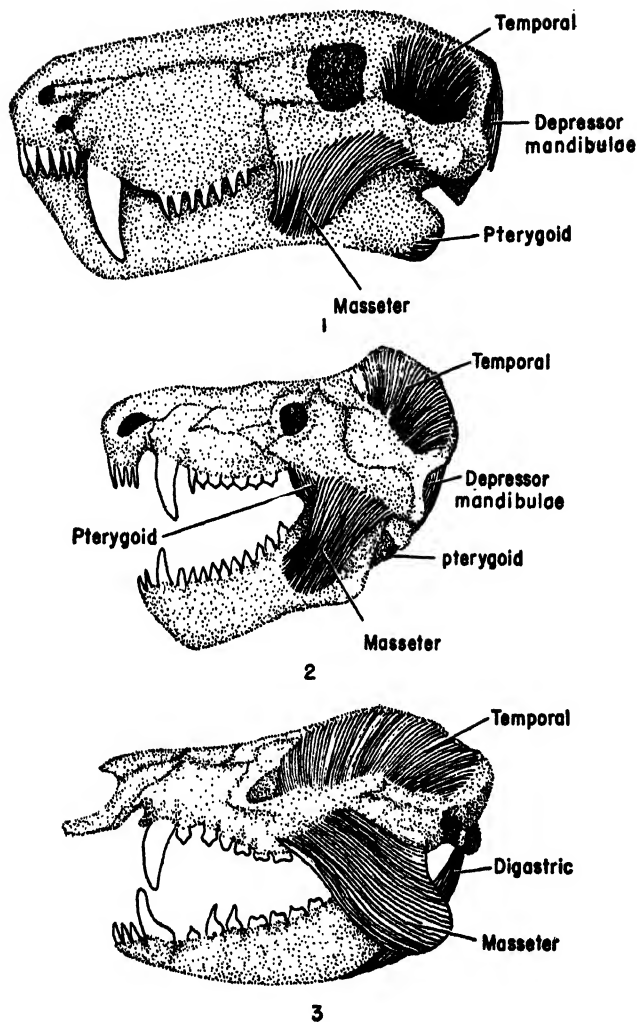


FIG. 119B. Evolution of jaw muscles. 1, primitive mammal-like reptile; 2, advanced mammal-like reptile; 3, opossum. (Redrawn from Gregory and Roigneau.)

The following branchiomic muscles are associated with the hyoid arch: the intermandibularis, already mentioned as associated with the lower jaw; the constrictor colli, derived from the facial constrictor; the constrictor of the pharynx, and the laryngeal muscles. The last two groups are derived from the constrictor. These muscles are supplied by the seventh cranial nerve.

The trapezius muscle, or dorsal and lateral continuation of the constrictor sheet, becomes of increasing significance with land life because of its action on the shoulder and on the head. It is attached to the thoracic spines and skull and inserts on the scapula. In mammals the sternocleidomastoid splits from it. The muscles are innervated by the tenth (vagus) and eleventh (accessory) cranial nerves.

Birds. In birds, branchiomic muscles innervated by the trigeminus (fifth cranial nerve) form two groups, (1) the constrictor dorsalis, which splits into a protractor pterygoideus and a levator bulbi, and (2) an adductor mandibulae, which separates into adductor mandibulae externus, internus, and posterior. Those innervated by the facial nerve are the depressor mandibulae, constrictor colli, and hyomandibularis medialis and lateralis. Associated with the tongue the glossopharyngeus and geniohyoideus muscles along the third visceral arch are supplied by the glossopharyngeal and the vagus nerve.

Mammals. The following description of the branchiomic muscles of mammals is based largely on that of Warren H. Lewis in Keibel and Mall's *Manual of Human Embryology*. The mammalian branchiomic muscles arise from the mesoderm of the branchial arches. It will be recalled that this primordium was derived from the hypomere rather than from the epimere, the origin of the remaining striated muscles. The branchiomic muscles are innervated by special visceral efferent nerves in contrast to the skeletal muscles, which are innervated by the somatic efferent nerves. Mesoderm from the mandibular arch gives rise to the muscles of mastication. These include paired masseters, temporals, external and internal pterygoids, and probably the mylohyoid (Fig. 120). This group is supplied by the fifth cranial nerve, the trigeminus.

The mesoderm of the hyoid arch gives rise to the facial muscles of expression: the platysma of the neck; the external ear muscles; the stapedius to the internal ear; the stylohyoideus and the digastricus; the levator veli palatini and the uvulae. This group is supplied by the seventh cranial nerve, the facial.

From the mesoderm of the third branchial arch the constrictors of the pharynx, the stylopharyngeus, and the palatoglossus originate. These muscles are innervated by the ninth cranial nerve, the glossopharyngeal.

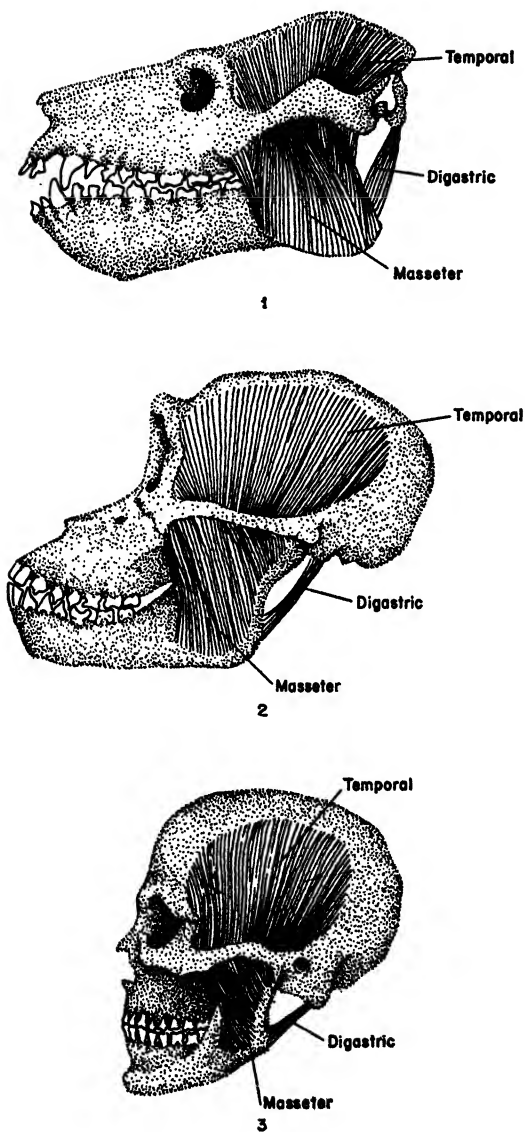


FIG. 120. Evolution of jaw muscles. 1, primitive primate; 2, chimpanzee; 3 man. (Redrawn from Gregory and Roigneau.)

The mesoderm of the remaining arches (part of the third and all of the fourth and fifth) is associated with the origin of the intrinsic laryngeal muscles, as well as with parts of the palatine and pharyngeal muscles. Belonging to the laryngeal muscles are three pairs of arytenoids and the cricothyroids. This group is supplied by the tenth cranial nerve, the *vagus*.

Trapezius and sternocleidomastoid muscles are probably caudal members of the branchial arch group. These two muscles are supplied by the eleventh cranial nerve, the spinal accessory, which is regarded as an offshoot of the *vagus* nerve.

The tongue muscles appear to be derived from occipital myotomes or directly from the mesoderm of the floor of the mouth and are not branchiomic. They are supplied by the twelfth cranial nerve, the hypoglossal.

The diaphragm apparently originates from a ventral muscle complex forming a "lingual-infrahyoid-diaphragmatic band," which according to Lewis is in no way related to the myotomic system.

APPENDICULAR MUSCLES

Amphioxus and Cyclostomes. Just how paired appendages arose in the vertebrates is unknown. The fin-fold theory, as observed, has been the most widely accepted explanation for their appearance (Fig. 83). According to this theory, lateral, continuous, integumental folds extending from the pharynx to the anus became interrupted and supported by cartilages, comparable with the relationships developed in the median fins. The anterior portion of the fold developed into the pectoral and the posterior into pelvic fins. The paired metapleural folds of *Amphioxus* are frequently cited as a possible clue to such an origin. Here the folds extend unbroken along the sides of the body from the gill region to the anus. These are folds of skin without underlying cartilaginous or bony support. Evidence based upon the study of fossil acanthodians, particularly *Climatius*, indicates that pectoral and pelvic spines antedated the appearance of movable fins. Supporting bars and fin membranes posterior to the spines were present in some. Gregory and Raven, Romer, Watson, and Stensiö have made important contributions to our knowledge of these fossil antecedents of the fishes, as was shown in connection with the description of the appendicular skeleton. It is hoped that their studies may eventually throw additional light on the appearance of muscles in association with pectoral and pelvic spines. Paired fins and lateral folds are absent in the cyclostomes.

Fishes. Lateral fin folds arise in the embryos of fishes, and appendicular muscles along with cartilaginous or bony supports grow into the

folds secondarily. These muscles arise from cells or from muscle buds at the ventral ends of the myotomes (Fig. 121A, B). When the muscles develop from buds, two muscle tabs appear at the ventral end of each myotome in the region of the lateral fold. The buds split tangentially into two layers, one of which passes dorsal and the other ventral to the skeletal elements of the limb primordium. In elasmobranch fishes, two to five basal cartilages extend into the fin from their articulation with pectoral or pelvic girdle. Distally several radial cartilages articulate with the basals. Beyond these, dermal rays reach to the extremities of the fold (Fig. 122A, B, C).

The dorsal muscle mass grows and expands over the skeletal supports. Its basal portion, as the extrinsic musculature of the fin, connects the latter with the trunk. Distally, intrinsic muscle slips extend over the

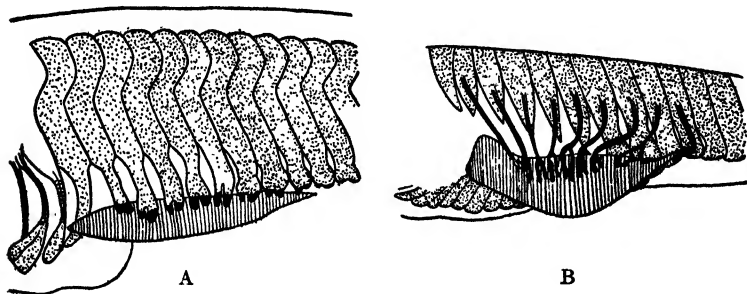


FIG. 121. A, the origin of appendicular muscles; B, further expansion of muscle slips originating from segmental body muscles. (Redrawn from Ihle.)

basal and radial cartilages. The dorsal muscle group becomes the common abductor, also known as the extensor of the fin. On the ventral side, similarly, a medial extrinsic muscle mass attaches the fin to the body, while distally an intrinsic portion covers the basal and radial cartilages. These muscles become the common adductors, also known as flexors of the fin.

Originally the nerves passing to the fin muscles are segmental. In the fish, however, beginnings of nerve plexuses are found. In the dogfish, for example, the ventral rami of some 11 spinal nerves pass to the pectoral muscles, and 10 pass to the pelvic. The anterior 4 or 5 pectoral nerves have cross connections, while the first nerve to the pelvic fin, the collector nerve, connects with adjacent spinal fin nerves.

This is the extent of the specialization of the fin musculature of fishes. It includes a generalized dorsal abductor or extensor mass and a ventral

adductor or flexor group with some differentiation of the anterior border of the ventral muscles to form a protractor of the fin.

Tetrapoda. The term *Tetrapoda* is a convenient designation for the great assemblage of land vertebrates, including amphibians, reptiles, birds, and mammals, with two pairs of land appendages rather than fins,

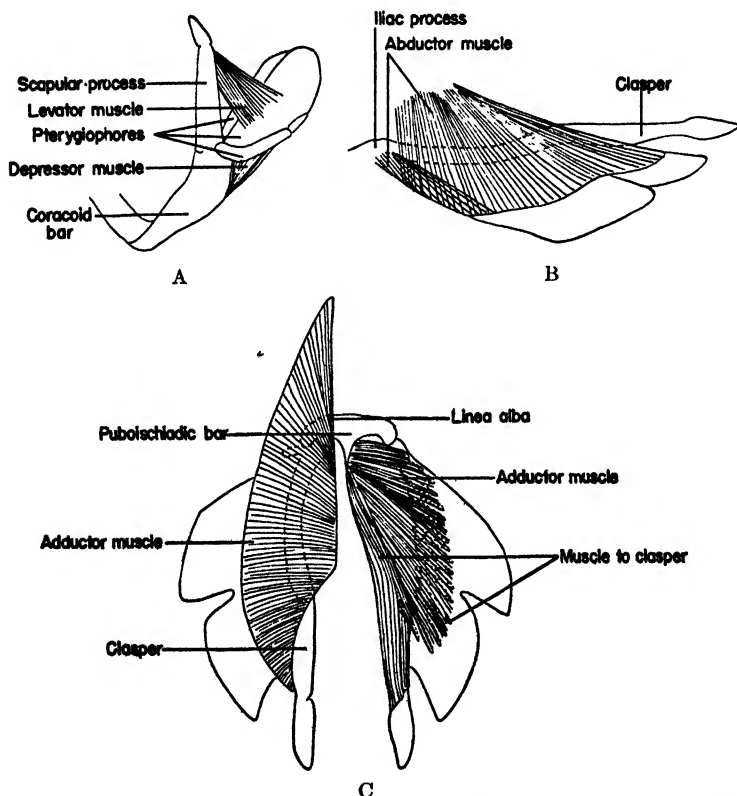


FIG. 122. A and B, differentiation of pectoral and pelvic muscles in the dogfish; C, muscles associated with pelvic clasper in male dogfish. (Redrawn from Ihle).

just as the term *Ichthyopsida* refers to the fishes and cyclostomes. Even superficial examination reveals an entirely different level of structure and function of limbs adapted for land and for air, as compared with fins. The land limb is a complex system of levers capable of a great variety of movement. In man, for example, there are over 50 individual

muscles in each upper and lower extremity, responsible for some 13 types of action.

As in fishes, the muscles of land limbs are arranged into two groups, an extrinsic, uniting appendages with the trunk, and an intrinsic, surrounding the appendicular bones directly (Figs. 113, 114). These muscles may be divided functionally into dorsal abductor-extensors and ventral adductor-flexors. Other functions become associated with these basic actions.

Amphibia. With the exception of the trapezius, which is of branchiomic origin, the extrinsic pectoral muscles arise from trunk myotomes. The chief dorsal extrinsic muscles are the latissimus dorsi, dorsalis scapulae, levator scapulae, trapezius, and pectoriscapularis. Ventrally the chief extrinsic muscle, the pectoralis, unites the sternum and upper arm. Associated with the coracoid and procoracoid bones of the pectoral girdle are the supracoracoideus and the procoracohumeralis muscles.

In the forearm and hand, differentiation of the original extensor and flexor mass results in the appearance of individual intrinsic extensors and flexors of the wrist and digits, such as the extensor carpi radialis, extensor carpi ulnaris, flexor carpi radialis, and flexor and extensor digitorum communis. This development is indicative of further specialization of these muscles in mammals.

The pelvic musculature shows a development comparable with that of the pectoral. On the dorsal surface of the pelvic girdle a puboischiofemoralis externus unites the puboischial plate with the femur. The ilium marks the origin for two muscles that insert on the tibia, the iliotibialis and the ilioextensorius. Ventrally a puboischiofemoralis internus, a puboischiotibialis, and a pubotibialis unite the trunk with the femur and the tibia. The intrinsic muscles are arranged as flexors and extensors on the shank and the foot. Three foot extensors lie on the dorsum of the shank. These are the extensor tibialis, extensor digitorum communis, and extensor fibularis, as well as short extensors of the digits. Flexors include gastrocnemius, soleus, and plantaris, together with a common flexor of the digits; the last, associated with a plantar fascia, also terminates on the digits.

Reptiles. Reptilian shoulder muscles show greater differentiation than do those of amphibians and resemble the mammalian shoulder muscles in distribution (Fig. 123A, B). A teres major splits from the latissimus dorsi; the cucullaris, or trapezius, splits off a sternocleidomastoid; the dorsalis scapulae, homologue of the deltoid in man, has clavicular and scapular divisions.

On the ventral side pectoralis and coracobrachialis constitute the adductors and biceps brachii and brachialis the flexors of the arm, while on the dorsal surface of the humerus the triceps brachii (anconeus) is the extensor of the forearm.

In the forearm the muscles are separated into flexor and extensor groups. The former take origin largely from the medial epicondylar

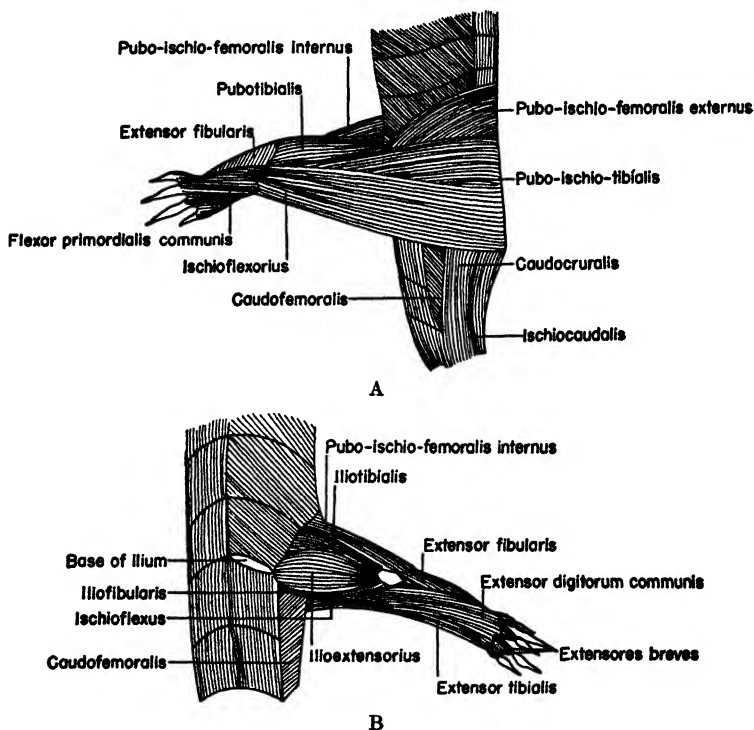


FIG. 123. *A*, lateral aspect of hind-limb muscles of a lizard; *B*, dorsal aspect of hindlimb muscles of a lizard.

region of the humerus and the extensors from the lateral epicondylar region of the same bone. As indicated, the general distribution of these muscles resembles that of mammals. Thus two flexors of the wrist, the flexor carpi radialis and the flexor carpi ulnaris, and two extensors, the extensor carpi radialis and extensor carpi ulnaris, lie in the forearm and terminate at the wrist. A common flexor of the digits, the flexor digi-

torum communis, and a common extensor, the extensor digitorum communis, act on the digits. Supination and pronation of the forearm are accomplished by specialized supinator and pronator muscles in the forearm.

The reptilian pelvic musculature is represented by long and short extrinsic muscles which connect the thigh with the trunk and by short intrinsic flexors and extensors overlying the femur, tibia, and fibula and foot bones.

Birds. In the shoulder girdle of birds the cucullaris, comparable with the trapezius and sternocleidomastoid of the reptiles, occurs (Fig. 124A, B). This extends from the occiput and the dorsal midline of the neck and back to the clavicle and skin of the shoulder. Rhomboid muscles unite the vertebral margin of the scapula with the neck vertebrae. Serratus muscles have split from the oblique abdominal muscle and pass from the lateral margins of the thoracic basket to the vertebral scapular margin. Stresemann divided the muscles of the upper and lower appendages of the bird into the following groups:

1. Cucullaris muscle, homologous to the trapezius and sternocleidomastoid of the reptiles. It connects head, neck, and back with scapula and clavicle.

2. Superior thoracic muscles, including rhomboids and serrati; the former connecting the neck with the scapula, and the latter extending from the sides of the thoracic basket to the vertebral margin of the scapula.

3. Inferior thoracic muscles, including only the sternocoracoid, originating on the sternum and ribs and inserting on the coracoid bone.

4. Inferior brachial muscles, which include two great antagonistic flight muscles, the pectoralis and the supracoracoid. The pectoralis originates on the sternum and inserts on the greater tuberosity and crest of the humerus. It pulls down and adducts the wing in flight. The supracoracoid also originates on the sternum under cover of the pectoralis and passes over the joint capsule to insert on the greater tuberosity of the humerus. This muscle, by pulley action, abducts the wing. Together these two muscles may constitute one-eleventh of the body weight of a strong flier like the wild duck.

5. Superior brachial muscles include the latissimus dorsi and the deltoids. They are extensors and abductors of the upper arm.

6. Extensors of the forearm and hand include the triceps brachii and the small extensors originating along the lateral epicondyle of the humerus, all supplied by the radial nerve.

7. Flexors of the forearm and hand include the biceps brachii and

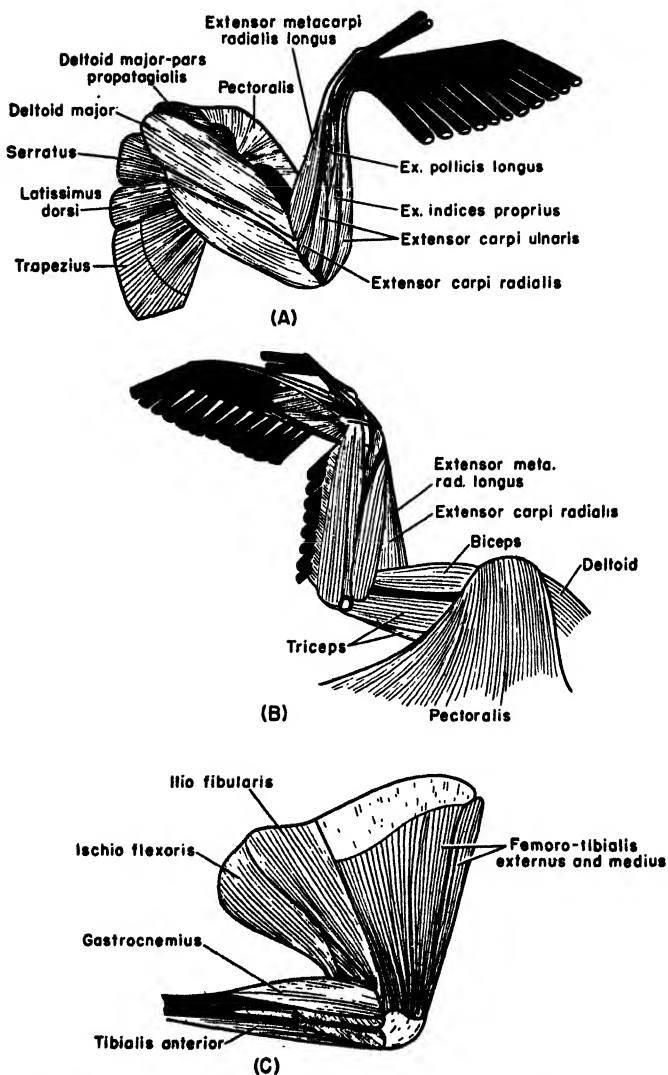


FIG. 124. Wing and leg muscles of the bird. (A), dorsal aspect; (B), ventral aspect; (C), leg muscles.

brachialis on the ventral surface of the humerus and the group of small flexors originating on the medial epicondylar region of the humerus and supplied by median, ulnar, and musculocutaneous nerves.

Pelvic Girdle

1. Dorsal iliofemoral muscles from the dorsal surface of the ilium to the greater trochanter and proximal end of the femur correspond to the gluteal muscles of mammals (Fig. 124C).

2. Internal iliofemoral muscles corresponding to the iliacus of mammals originate on the internal surface of the ilium and insert on the proximal end of the femur.

3. The ambiens muscle extending from the pelvic rim to the patella is homologous to the extensor tibialis in reptiles. This muscle, absent in many birds, when present acts as an extensor of the tibia.

4. The obturator-adductor group on the medial side of the thigh originate on the rami of pubis and ischium and insert on the medial side of the femur. They are the great adductors of the thigh.

5. Extensors of the leg originate on the femur and insert on the tibia and extend along the shank.

6. Caudoiliofemoralis connects the base of the tail with the femur. Because of this direct connection, the side-to-side motion of the tail is brought about in many strutting birds.

7. Adductors of the shank correspond to the semitendinosus and semimembranosus of the mammals. They originate on the ischium and insert on the medial side of the tibia. They include the ischioflexorius, the caudoilioflexorius, and the iliofibularis.

8. Foot and digital extensors include the tibialis anterior; the extensors of the first, third, and fourth digits; the abductor of the second digit; the extensor digitorum communis; and the peroneal longus and brevis.

9. Foot and digital flexors include the gastrocnemius and the long and short flexors of the digits.

Mammals. In mammals the pectoral support for the upper limb consists of a scapula and usually a clavicle, although the latter may be absent in ungulates or vestigial in carnivores. The muscle-skeletal arrangements of the girdle are such that the shoulder may be rigidly braced against the body, or it may be held loosely and actively moved. The scapula may be elevated or depressed; it may be adducted to the middorsal line, abducted, or rotated.

A group of extrinsic muscles attaches the scapula and clavicle to the trunk and head (Fig. 125A). Dorsally these muscles include the trapezius, sternocleidomastoid, levator scapulae, and rhomboids. On the

ventral side are the subclavius, pectoralis major and minor, and serratus ventralis.

Uniting the scapula or the trunk with the humerus are latissimus dorsi, teres major and minor, supraspinatus and infraspinatus, subscapularis and triceps brachii (long head), coracobrachialis, and deltoid. The above groups account for the flexor, extensor, abductor, adductor, rotator, and circumduction actions of the upper arm and shoulder.

Originating from the lateral epicondylar regions of the humerus are several intrinsic extensors of the wrist and digits. These lie on the dorsum of the forearm and insert variously on the wrist and digits. From the medial epicondylar and ulnar region a comparable group of flexor muscles takes origin. These pass over the ventral surface of radius and ulna and insert variously on the palmar surface of the wrist and digits.

In the hand individual abductors, adductors, extensors, flexors, and opponens muscles appear and become associated with the forearm and wrist (Fig. 125*B*). This differentiation of hand musculature reaches its greatest development in the human being.

The mammalian pelvic girdle is more firmly anchored than is the pectoral. The innominate bones are united with the sacrum by ligaments, permitting little free movement at the articulations. The innominates are quite firmly joined with each other by pubic and in many mammals by ischial symphyses.

Extrinsic muscles, both dorsal and ventral, unite the femur with the pelvis (Fig. 126*A*). Dorsally three gluteal muscles, tensor fasciae latae (caudofemoralis in tailed animals), piriformis, and gemelli serve this function. Ventrally three adductors of the thigh, and associated with them two obturators, unite the pelvis with the femur. Muscles that extend and flex the shank lie on the ventral and dorsal surface of the thigh, respectively. The great quadriceps femoris, composed of four separate muscles originating on the pelvis and the shaft of the femur and inserting on the patella, which in turn attaches to the tibia by the patellar ligament, is the chief extensor of the shank. Dorsally semitendinosus, semimembranosus, and biceps femoris are the chief extensors of the shank. They originate on the ischial tuberosity with the exception of one head of the biceps, which arises on the shaft of the femur, and they insert on the proximal ends of tibia and fibula.

On the anterior and lateral surfaces of the shank are located the extensors and abductors of the foot and digits; on its posterior surface are comparable flexors and inverters (Fig. 126*B* and *C*).

A survey of vertebrate appendicular muscles reveals a gradual in-

crease in differentiation and an evolution of function, leading to increased action and variety of movement of the extremity. In the generalized hand and foot this increased function is associated with a large number of intrinsic muscles. In the specialized limb of the horse, on the other hand, a reduction of muscles and skeletal parts has led to highly restricted actions.

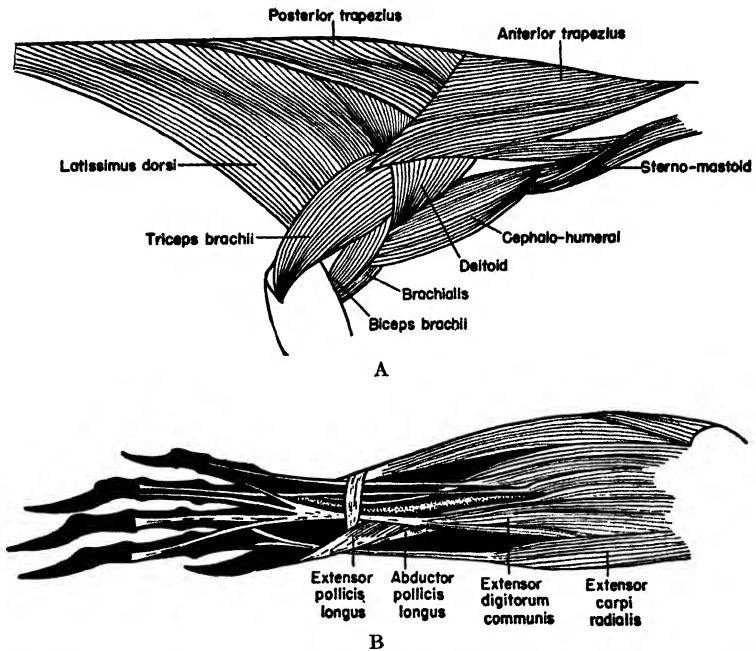


FIG. 125. A, shoulder and upper arm muscles of the rabbit; B, forelimb muscles.

ELECTRICAL ORGANS

Living protoplasm has electrical properties associated with it. One of these properties may be expressed as difference of electrical potentials between one part of the cell and another or as electrical-potential difference between one part of the body and another. The activities of the nervous system are partly electrical whatever else they may include. The fact that muscle, gland, nerve, and blood stream build up potentials in relation to their environment, even though these differences be small, indicates the possibilities of such a system. If an organ can be built up

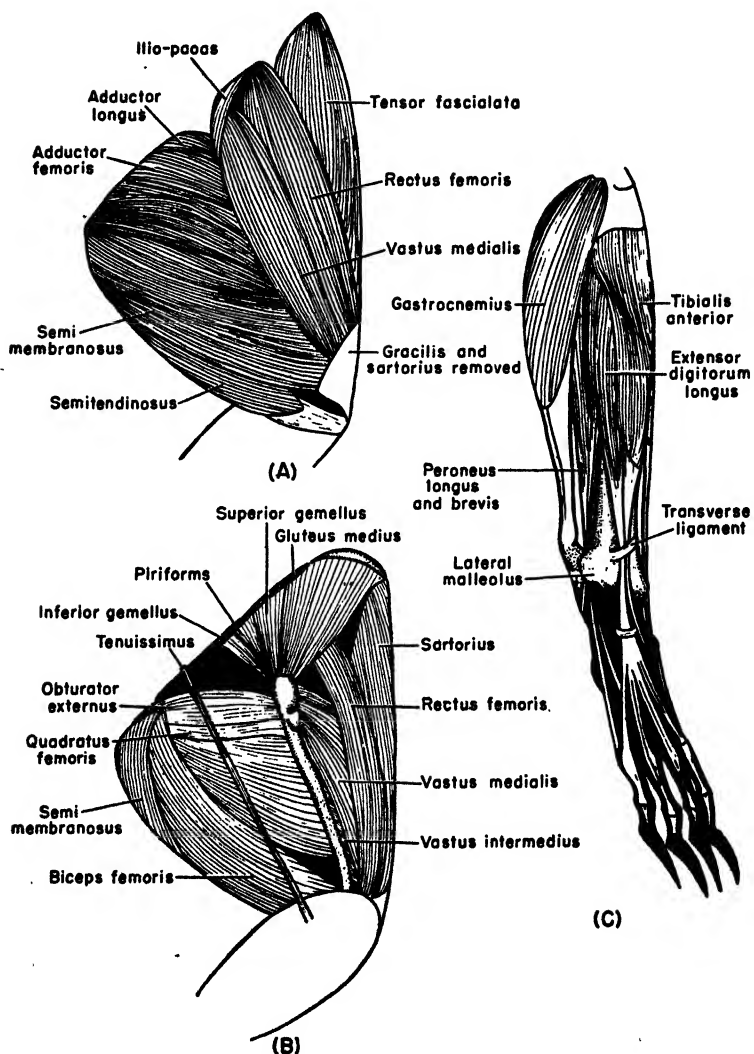


FIG. 126. Thigh and hindlimb muscles of the rabbit. (A), medial aspect of thigh muscles; (B), thigh muscles, deep level; (C), right hind leg.

by a serial arrangement of plates each capable of taking up a small charge and able to discharge collectively to a conductor, an effective electrical shocking mechanism may be produced. This has happened in several instances among the vertebrates. In three types of development of electrical organs the systems apparently arose independently of each other.

The following account is based largely upon that of Ihle, who has pointed out that the probable explanation for the appearance of electrical organs in the elasmobranchs and the teleosts is to be explained by the fact that electrical organs require a good conduction medium; hence their appearance is confined to aquatic types.

Electrical organs in the elasmobranchs and the teleosts presumably arose independently, as noted, although in both instances they involved transformation of muscles. An exception is the organ in the teleost *Malapterus*, where it is of glandular origin. In the elasmobranch the innervation of the electrical organ by cranial nerves 7, 9, and 10 point to an origin from visceral muscles. In the electrical eel, a teleost, the electrical organ extends along the sides of the body and has involved transformation of a large part of the hypaxial musculature. The organ may constitute as much as one-third of the body weight of the animal. The mechanism is supplied by some 350 spinal nerve fibers. In *Astrocopis* the organ appears to arise embryonically from the eye musculature and is supplied by a branch of the oculomotor nerve. In *Malapterus* the electrical apparatus originates from gland cells in the skin. It is supplied by a pair of nerves originating in two large ganglia in the spinal cord just caudal to the medulla oblongata.

In spite of differences in origin the general nature of the mechanisms is basically similar in the various species in which it appears. It occurs in 15 species of 7 genera of the Torpedinae as well as in several species of the genus *Raja* and in several teleost genera. In *Torpedo* it consists of a series of plates arranged one upon the other to form a total of 600 columns. Each column may be built up of some 400 plates. In structural detail the two sides of a plate differ from each other. One face is smooth and covered by a thin epithelial tissue called the electrical cell layer; the other face has a series of papillae extending into the surrounding connective tissue. These papillae lie in close proximity to the nutrient blood vessels. The nerve supply extends to the smooth face and may terminate in a delicate end net. During electrical discharge this face of the plate is negatively charged. The plates are separated from each other and immediately surrounded by a characteristic electrical connective tissue of about the same thickness as the plate. They are

further held in position by connective tissue septa, which envelop the electrical layer and the plates themselves. Each plate builds up a small charge, and the electrical shock results from the simultaneous discharge of this battery. A nerve stimulus or, presumably, reflex action serves as the trigger for the discharge.

The source of the potential differences built up in the electrical organ of fishes is undoubtedly the oxidation within the plate or the immediately surrounding electrical connective tissue. Presumably the papillary face and its close proximity to the nutrient supply are the chief contributing factors in building up the charges.

The nature of this battery and its dependence upon oxidation recall a comparable system constructed by the late Dr. George Crile. He built a voltaic pile or simple battery of the halves of apples arranged serially. The mechanism had "a potential difference of approximately one volt, sufficient to light a tiny electric bulb."¹ In that experiment he determined that the potential difference of the pile could be modified by changing the oxidation rate of the apples.

MUSCULATURE AND LEVELS-OF-BEING CONCEPT

A careful comparison of the musculature of the chordates beginning with the Cephalochordata and ending with the Mammalia shows distinct levels of development. Living chordates are the survivors of a long-protracted struggle for existence. The successful have benefited from adaptive mutations affecting musculature as well as other body systems in which the possibility for future change is inherent.

Water-inhabiting chordates, the cephalochords, cyclostomes, fishes, and aquatic amphibians, reach the same general level of muscular development. Their habitat apparently determines the segmental arrangement of their musculature. This effect of habitat on muscles is shown in mammals which have returned to an aquatic life. The whale and porpoise, the sea cow, and, to a lesser extent, the seal and walrus show some return to a generalized body musculature, with loss or modification of the land limbs making them roughly comparable to the fish in body architecture. In the case of the first three the tail flipper, horizontally placed, is moved up and down by generalized epaxial and hypaxial muscles.

Land-inhabiting chordates that support and transport their bodies upon appendicular lever systems constitute another distinct level of muscular development. While great differences exist in the musculature of reptiles compared with mammals, the general pattern shows many similarities.

¹ *The Phenomena of Life*, p. 53, W. W. Norton & Company, New York, 1936.

The small running lizard has developed a successful appendicular apparatus which conveys its body with considerable speed. From some such beginnings the great locomotor systems of ungulates and carnivores evolved. The last two groups stand at the peak of achievement in land locomotion. Added to the purely locomotor functions are various adaptations for maiming and killing, placing their possessors on unique levels of physical performance.

Birds represent another level of muscular achievement. The air has adopted them. This has been brought about by fortuitous mutations that produced an orderly adaptation of skeleton, body form, integument, eye, and a respiratory system to the exacting medium of the air. The great pectoral muscles have become the dominant muscular organs. Other muscles may be discarded, excess weight is eliminated, and vision supplants smell. The resulting mechanism is acceptable to the air.

The Primates, while they do not excel in speed, have made perhaps the greatest gains through their musculature. Because of their tree habitat, primates were able to compete with their swifter mammalian relatives on the ground. The tree also helped to free the forelimb from its exclusive weight-bearing function. This modification entailed changes in the motor cortex of the brain. The freeing of the hand and its consequent development contributed in no small part to man's commanding position on the earth.

In the above description smooth, striated, and heart muscle have been treated as though they differ only amongst themselves and not within themselves. Comparisons of striated muscles in fish, reptile, carnivore, and primate, however, reveal great differences in blood supply, in iron content, and consequently in work capacity.

The striated muscle of fish is white or pink; that of reptiles is generally a rich pink. In the turtle, however, it becomes red, owing to greater vascularization. Kükenthal states that white muscle in the bird is capable of more rapid contraction than red; it yields more breakdown products, it tires more easily, it develops more heat. The red is used primarily in maintaining balance. He believes that the plentifulness of hemoglobin and cytochrome (myohematin) in the red muscles act as catalysts supporting oxidation during prolonged contractions. Seal, white whale, and walrus have a striated musculature that is almost black because of iron content and great vascularization. When the author first opened the arctic white whale, this condition was plausibly explained by the high metabolism, or rate of living, necessary to maintain these animals in their icy surroundings. In like manner the light-pink musculature of the sea cow, another aquatic mammal that was captured in subtropical waters, could be understood in terms of its

habitat and food habits. The heart, for example, of a 420-kg. (935-lb.) sea cow weighed 1,250 gm. compared with a 2,454-gm. heart of a 421-kg. (940-lb.) white whale. The blood volume shows corresponding differences.

Other factors also control muscle action. The amount of thyroidization and adrenalization, for example, may not be ignored in evaluating the work output or the metabolism of striated muscle.

In its activity, muscle is regulated by systems outside itself, and it has become so dependent upon these systems that of itself it is helpless to act. It has been pointed out that a muscle separated from its nerve supply is paralyzed and soon undergoes degenerative changes involving conversion of substance into a useless fibrous tissue. It represents a subordinate system integrated with and subservient to the whole and yet with considerable influence on the degree of well-being of the whole. A grievous muscle wound affects more than muscle, just as a well-developed muscular system influences other parts.

The dissector interested in muscular function or in energy release in animals becomes aware, as noted, of great differences in muscle coloration due to variations in vascular supply, in their length and distribution, and in muscle attachments. All these features provide clues to the level of performance attained by an animal.

The fish may present as much as 70 to 80 per cent of its mass as muscle, and although the animal is cold-blooded, this muscle mass by its primitive arrangement into metameric muscle segments can perform considerable work. The aquatic vertebrate almost invariably runs to muscle.

In the land amphibians, specilization of muscles and skeleton has produced elaborate lever systems as well as reduction in the percentage of muscle to body mass. In the frog, for example, muscle is largely concentrated in the appendages.

In the reptiles several patterns are apparent. That of snakes simulates that of aquatic forms, *i.e.*, a generalized type of muscle again increasing in proportion to the body mass and correlated with their peculiar type of locomotion. In the turtles, on the other hand, a reduction in percentage of muscle takes place with adoption of a series of leg levers, and, what is equally significant, great increase in vascularization. It has been pointed out that the muscle of turtles appears as red as that of mammals, while that of the Crocodilia and Squamata is pale and fish-like. These conditions are secondarily reflected in the heart development in these three suborders.

Birds have acquired an additional advantage in energy utilization, besides lightness of bone and body covering of feathers. That advantage

is high body temperature, which when combined with their peculiar type of respiratory apparatus confers great advantages in the capture of oxygen and the subsequent release of energy. Muscle is concentrated largely for running and for flight.

Mammals, which from the standpoint of muscle and skeleton are complex mechanisms adapted for energy spending, show a variety of specializations and adaptations in this respect. Thus the actual position of the limbs, their relative size, the amount of blood, size of the heart, vital capacity—all point to the end of energy release through the muscular-skeletal lever systems.

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CHAPTER 6

THE NERVOUS SYSTEM

ROLE AND NATURE OF NEURAL ACTIVITY

The nervous system is the executive center of the animal body, a function it shares with the endocrine glands, without whose secretions and humors the other system is incapable of normal action.

To the nervous system are referred the myriad problems which confront the organism from within and without. Brain and cord accept these problems, which appear in the guise of stimulations; they resolve them in action, store them in memory, or, if the stimulus is too great, may be so completely baffled that they abdicate their executive functions momentarily and leave the body at the mercy of the external or internal forces working upon it. Ordinarily the central system responds to the environment if proper sensory receptors that can appreciate the external and internal world are present, and it is by this means that its great value to the animal is asserted. Its constant activity and vigilance maintain the body in the great stresses of life as well as in the solution of problems that confront it from moment to moment. Such activities as heartbeat, respiration, eye movements, intestinal motility, thought, to mention but a few, are indicative of its all-pervading influence.

The key to an understanding of this controlling mechanism and of the level of being that the animal ultimately achieves is to be found in the degree of development of the nervous system and the endocrine glands. It has been pointed out repeatedly that, in the evolution to higher levels, all body parts cooperate; muscle and skeleton, heart and glands, brain and sensory organs, for example, all show correlated advances.

The operation or activity of a nerve cell is an involved process, dependent upon electrical changes in its substance and along its course. When stimulated, for example, it shows a change of electrical potential along its fiber (Fig. 127). The frequency and intensity of these oscillations are correlated with the intensity of the stimulus, the state of the nerve cell, or the amount of oxygen available to it. Apparently the conduction is chemicoelectrical. We have no reason, on the basis of

the evidence, for believing that awareness resulting from stimulation is other than this. The studies of Adrian in England and Bronk, Bishop, and others in this country have made an excellent start in determining some of the physical phenomena that accompany or are responsible for nerve activity. Various brain regions studied from this viewpoint indicate that the hippocampus, for example, may set up slow spontaneous potential waves and, when stimulated, develop waves of greater frequency, that are transmitted to other parts of the nervous system.

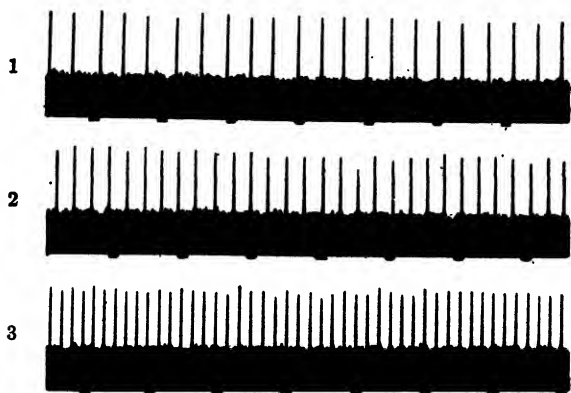


FIG. 127A. The effect of increasing pressure on a pressure-sensitive ending. The effect is recorded in terms of electrical oscillations which are conducted along the sensory nerve fiber. The pressure is successively greater in 1, 2, and 3. (Redrawn from Bronk.)



FIG. 127B. The position of the electrode in the midst of small vessels on the surface of the cerebral cortex. (Redrawn from Bronk.)

Fundamental and significant as these new findings are, it is difficult to reconcile oneself to the idea that mental activities, including rational thought, are nothing more than chemico-physical disturbances.

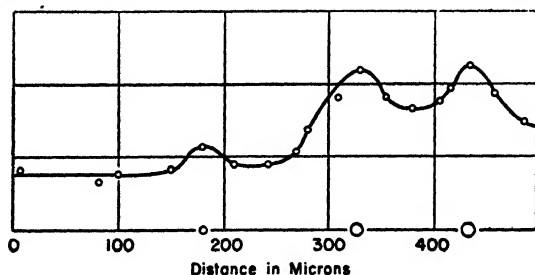


FIG. 127C. Variations in oxygen concentration correlated with distance of the oxygen electrode from the vessels. Positions of a vein and two small arteries are indicated on the axis of the abscissae. (Redrawn from Bronk.)

THE NERVE CELL

The structural unit of the nervous system is the nerve cell, or *neuron*; the functional unit is the *reflex arc* (Figs. 128, 129). The nerve cell has a cell body containing a clear *nucleus*, *nucleolus*, and *cytoplasm*. In the latter are *glycogen granules*, *mitochondria*, *chromophil* or Nissl bodies, and a *Golgi network*, all related to the function of the cell. Two processes normally extend from the cell body: one, the *dendrite*, of delicate fibrils, a cytoplasmic extension; the other, the *axon*, or neurite, of neurofibrils combined in a single fiber, which may have collateral extensions. The axon differs structurally from the dendrites and the remainder of the cell, since Nissl bodies do not extend into it as they do into the dendrite. Another distinction is the *axon sheath*, or cylinder, which is absent from the dendrite. It makes synaptic junctions with dendrites of other cells, which are naked and gray, as is the cell body. The synapse has been designated as the anatomical site of the integrative action of the nervous system and the white substance of the axon the conducting mechanism from one center to another. Conduction impulses pass from dendrite to cell body to axon.

The several types of neurons include *unipolar*, *bipolar*, and *multipolar* cells, the latter of two kinds. *Unipolar* cells have only a single process associated with them. Whether these are axons or dendrites is not clear; they are more plentiful in invertebrates and lower chordates. According to Maximow and Bloom they also occur in the mesencephalic nucleus of the fifth cranial nerve in man. In the *bipolar*

the two processes may appear as one as they leave the cell body, but they divide shortly after leaving it; more typically they project from opposite ends of the cell. One type of *multipolar* cell is characterized by numerous collateral, or side, branches from the axon, in synapse with a number of dendrites. In the other type the axon splits into a

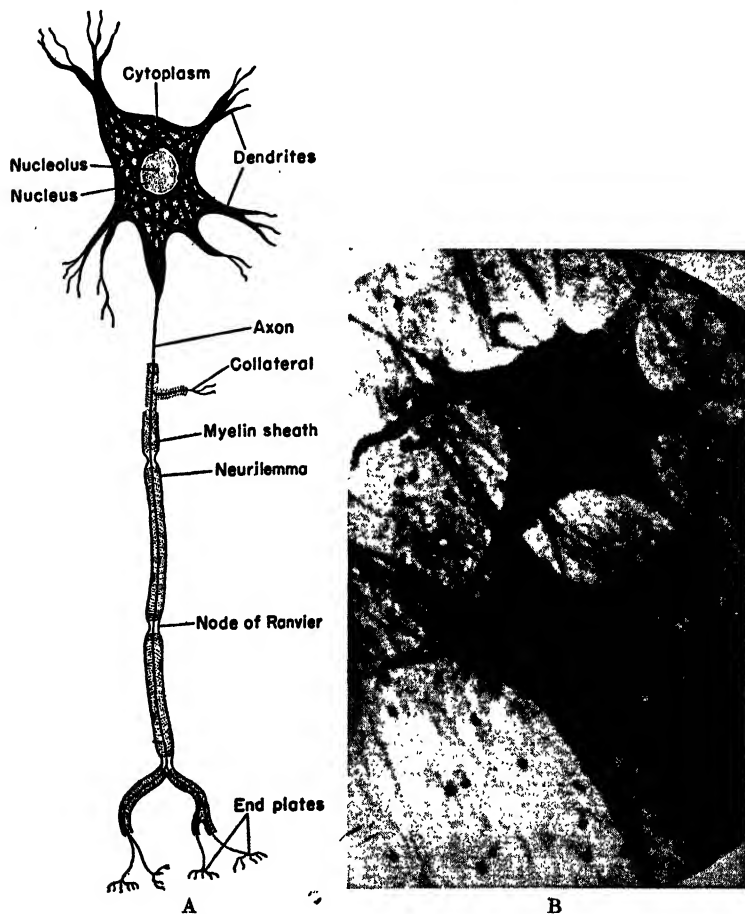


FIG. 128. A, diagram of a nerve cell; B, photograph of a giant motor nerve cell in the spinal cord of a mammal. (B, Courtesy of the General Biological Supply House, Chicago.)

number of branches upon leaving the cell body. These again are in contact with other cells.

Supporting the nerve cells are *neuroglial cells* of various types, binding together the colloidal nerve tissues. Embryonically they are derived from *spongioblasts* in brain and cord. The spongioblasts in turn give rise to *ependymal cells*, or star-shaped cells with many dendrites, and *oligodendrocytes*, or supporting cells with few processes. *Microglia* of mesodermal origin, in contrast to the ectodermal origin of the previously mentioned types, also occur. These small ameboid and phagocytic cells appear in large numbers at the site of nerve injury or infection. They are frequently involved in brain tumors. Their

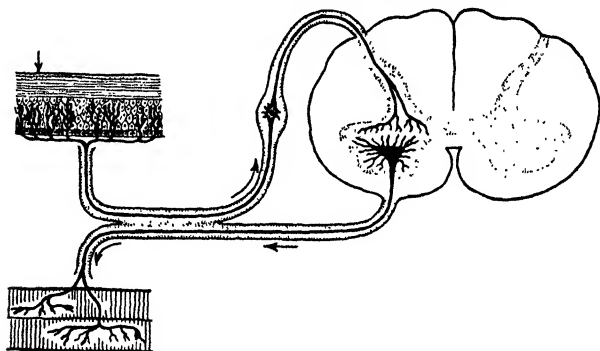


FIG. 129. A reflex arc. The impulse is initiated in a sensory ending and traverses an afferent nerve. The dendrites of such nerves synapse with axons of motor-nerve cells, and the impulse travels to the muscle via the latter.

more primitive nature apparently makes them susceptible to uncontrolled growth.

Functionally, nerve cells are designated as *sensory*, or afferent, leading impulses to the central system; *motor*, or efferent, directing impulses away from the central nervous system; and *association cells*, which unite the other two. *Somatic sensory* cells receive impulses either from the surface or from muscles and articulations within the body. *Visceral sensory* nerves receive impulses from various internal organs and mucous membranes. *Somatic motor* nerves convey impulses to voluntary muscles, while *visceral motor* nerves carry them to smooth muscles, vessels, and glands. These last are the motor elements of the autonomic nervous system.

Nerve impulses are conducted typically in one direction along the cell and its processes; they pass along the afferent dendrite to the cell body,

thence through the efferent axon. This mode of transmission indicates a polarized state of the cell. The axon terminates in an arborization in contact with the dendrite of another cell, called the *synapse*. This contact is not continuous, and a certain amount of resistance and a time lag are experienced when an impulse traverses a synapse. As indicated, the axon is commonly covered by a fatty insulating layer, the myelin sheath, which gives a characteristic white appearance to the sectioned fiber. Naked gray fibers occur chiefly in sympathetic nerves.

MENINGES

Meninges are supporting and protective tissues for the brain and cord (Fig. 130). They form three connective-tissue envelopes around the

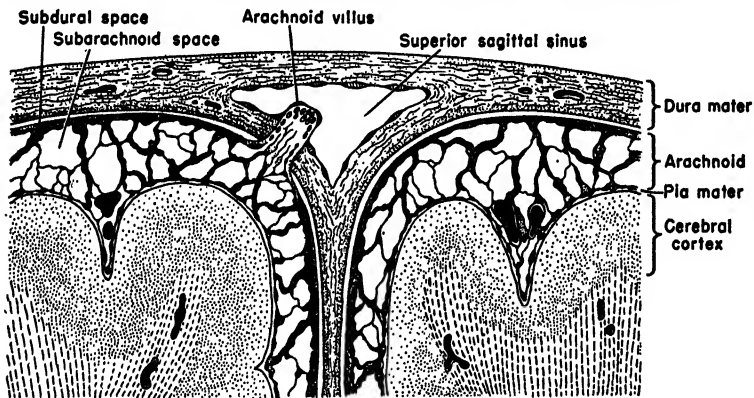


FIG. 130. The meninges of the brain. The tough dura mater covers the delicate net-like arachnoid, which in turn surrounds the delicate pia mater. (Redrawn from Cunningham.)

central nervous system. Beginning with the outermost they are the *dura mater*, thickest and toughest and most highly vascular and inelastic of the three; the *arachnoid*, thin and generally without much vascular supply; the *pia mater*, closely adherent to brain and cord, with a fine meshwork of vessels. The dura actually is the lining, or internal periosteum, of the skull and vertebral column and serves also as a protective membrane for brain and cord. It is made up of two fused layers, an endosteal adherent to the bone; an inner, or meningeal, smooth and lined with epithelium, which faces the arachnoid. The dura is well supplied with meningeal vessels derived from external and internal carotid arteries. The great venous sinuses which drain the blood from the brain also lie between the endosteal and meningeal layers, together

with the smaller meningeal veins which drain the dura proper. In the cord the two dural lamellae are separated; the endosteal forms the periosteum lining the neural canal, and the meningeal loosely covers the cord. The cavity between them is the *epidural space*. Venous plexuses, which reach amazing proportions in the Cetacea, are in the dura, while dural sleeves surround the dorsal and ventral nerve roots as they emerge from the neural canal.

The arachnoid, or middle layer, a thin fibrous membrane, surrounds both brain and cord. It is poorly supplied with blood vessels. The *subdural space* is between dura and arachnoid; that between arachnoid and the underlying pia mater is the *subarachnoid cavity*. Pia mater and arachnoid are connected by *trabeculae* that apparently increase the diffusive and absorptive powers of the membrane and aid in retention of the spinal fluid. *Arachnoid villi*, small reddish elevations, push into the outer dural layer and end in the sagittal and other sinuses of the brain.

The delicate pia mater, closely associated with the surface of brain and cord, consists chiefly of minute *vascular plexuses*. It follows the gyri of the brain, and in the cord, where it is firmer, it is also a supporting membrane. Both arachnoid and pia mater surround the cranial and spinal nerves to their points of emergence from the skull or the neural canal.

CEREBROSPINAL FLUID

Of great significance to the welfare of brain and cord is the cerebrospinal fluid. This is either secreted by or filtered into the brain ventricles and the subarachnoid space by the *chorioid plexuses* (Fig. 131). The latter line the lateral ventricles and the roof of the third and fourth ventricles. In the lateral ventricles the plexus consists of highly vascularized fringes of pia mater lined with ependymal epithelium. In the roof of the third and fourth ventricle the chorioid plexus projects into the ventricular cavities. With its pial covering it is called the *tela choroidea* of the third and fourth ventricles. Throughout, the chorioid plexuses are lined with ependymal cells continuous with those of the ventricles and the neural canal.

The cerebrospinal fluid passes from the lateral ventricles by the inter-ventricular foramina into the fourth ventricle. Here fluid from the neural canal also enters. The fluid then enters the subarachnoid spaces by an opening over the fourth ventricle, the foramen of Magendie, and by the lateral foramina of Luschka. It reenters the blood stream through absorption by the tuft-like arachnoid villi projecting into the venous sinuses of the brain.

PHYLOGENETIC ORIGIN OF THE NERVOUS SYSTEM

Irritability is an inherent characteristic of protoplasm. For this vague inclusive term *irritability* we shall probably someday substitute the term *polarization*, or electrical imbalance, which describes the condi-

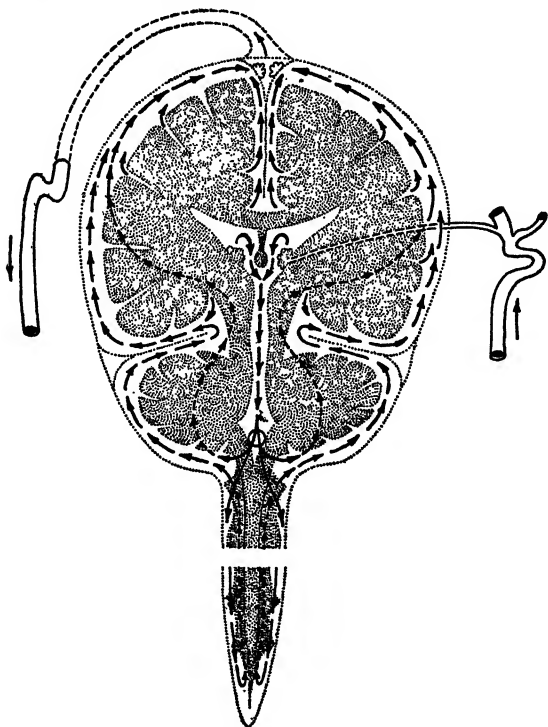


FIG. 131. Cerebrospinal fluid circulation. The fluid secreted in the chorioid plexuses of the brain circulates through the ventricles and escapes into the cord and the brain surface by the foramen of Magendie. It is reabsorbed into the venous channels of the brain through arachnoid tufts which project into the lumens of the vein. (Redrawn from Cunningham.)

tion in the nerve cell more accurately than does the earlier term. This electrical imbalance, or irritability, is the result of an early phylogenetic evolution in which specialized cells appeared, whose chief function was to accept and transmit impulses from the internal and external environment.

Although thread-like processes, the *myonemes*, whose presumable

function is the transmission of impulses, occur in ciliate Protozoa, the first true transmitting cells appear in the integument of the Coelenterata (Fig. 132). In the ectoderm of Hydra, and derived from it, are scattered *neuroepithelial cells* with processes extending into the jelly-like mesoglea underneath. These cells in turn join *primitive ganglion* cells arranged in a loose network between ectoderm and endoderm. The primitive

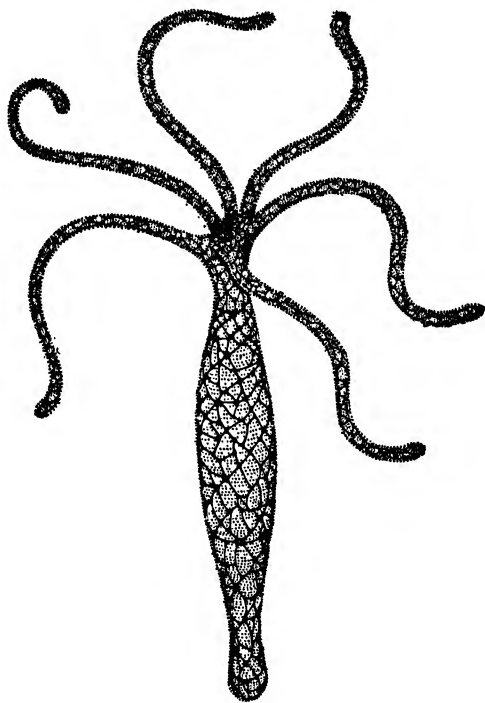


FIG. 132. The nerve net of hydra. Hydra has a diffuse nervous system covering the body and tentacles. A small stimulus may be quickly spread over the network.

ganglion cells connect with extensions from another group of ectodermal derivatives, the *musculoepithelial cells*. Such a system, although far removed in structure and complexity from that of the mammal, shares certain features with it. Through it the organism may respond to impulses from without or within, since they are transmitted throughout the network and evoke a widespread response. The primitive ganglion cells anastomose with each other, in contrast to the synaptic junctions

between nerve cells in higher animals. However, in some Coelenterata (Scyphomedusae, jellyfish), synaptic functions have been demonstrated.

Concentration of ganglionic material establishes a brain and longitudinal nerves, the latter comparable to a nerve cord, in the invertebrate round- and flatworms. This is an advance over the primitive nerve

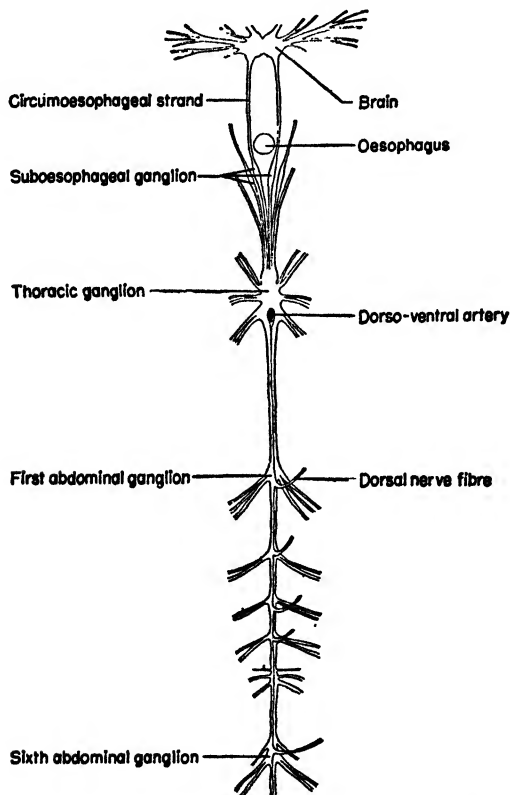


FIG. 133. The nervous system of the marine crayfish *Panulirus argus*. The system is concentrated in a brain, ventral ganglia, and cord with peripheral distribution from these centers.

net of the coelenterates. At the annelid level, a sensory apparatus, a pair of dorsal ganglia and a double ganglionated chain extending the length of the body underneath the digestive tract, constitutes the nervous system. In the arthropods the system is highly organized (Fig. 133). In vertebrates, brain and cord lie dorsal to the digestive tract, and nerv-

ous functions are essentially similar to those of higher invertebrates, with the gradual addition of psychic qualities.

THE DEVELOPMENT OF THE NERVOUS SYSTEM

For description, the vertebrate nervous system may be separated into central, peripheral, and autonomic divisions. The central system is made up of the brain and cord; the peripheral includes cranial and spinal nerves; the autonomic, sometimes considered part of the peripheral, includes sympathetic and parasympathetic subdivisions.

The central nervous system originates from the ectodermal neural plate along the middorsal line of the embryo. This plate becomes folded so that its lateral margins meet and fuse in the midline and become overgrown by the surface epithelium. The resulting tubular arrangement of nervous tissue along the middorsal axis has neural crests, also of ectodermal origin, and lateral to the line of fusion. These differentiate into sensory ganglia. A medullary canal resulting from closure of the plate becomes the central canal of the cord, while its anterior expansions are the ventricles of the brain. With the closure, differentiation appears in the neural tube. Lining it are secretory, columnar ependymal cells that are ciliated in the embryo. Outside of these a mantle layer of neuroblast and germinal cells is destined to become functional nerve cells centered chiefly in the gray matter of the cord. The outermost layer of the cord, a marginal network without nuclei, supports the columns of medullated fibers that now appear in the cord as ascending and descending tracts. These will be described later. Developed from the ependymal layer, as indicated, are various types of neuroglial cells which with their processes support the gelatinous nerve cells.

THE SPINAL CORD

Functions. Before attempting a description of the structure of the spinal cord, this brief account of its functions may aid in understanding the involved structural relationships.

The cord has two sets of basic functions: one relates to activities more or less independent of the brain, the other to the transmission of impulses by its nerve tracts. These place various divisions of the brain in communication with different regions of the body.

Its independent activities are carried on through spinal reflexes in which an afferent (sensory) nerve transmits an impulse to the cord. The distal ending of this sensory nerve is united with a sensory corpuscle or organ, while the proximal is in synapse with association cells that

communicate with motor cells. The motor-cell axons as efferent nerves convey the impulse to the musculature without necessarily involving the brain. The cord controls many activities of glands, visceral organs, and voluntary muscles through such reflexes.

As a conducting pathway it receives more than a half million sensory fibers combined in the various dorsal nerve roots of man. These are arranged into ascending tracts which may terminate in the cord, medulla, cerebellum, or cerebrum. From these brain centers descending (motor) tracts pass via the cord to the motor roots of the various spinal nerves. These tracts constitute the white (myelin) matter of the cord. The gray matter includes the bodies of association and somatic motor cells, the dendritic portions of such cells, and the bodies of visceral motor cells.

Structure. With continued growth of the embryo, further differentiation occurs in the central system. The cephalic portion of the medullary tube forms the brain; that in the body, the spinal cord. In the human being, the neural tube anterior to the first eight somites becomes the brain; that posterior to the eighth somite, the cord. For the detailed development of these parts the reader is referred to textbooks on embryology.

The mammalian cord is a somewhat flattened cylindrical mass of nerve fibers arranged in fasciculi, or bundles; nerve-cell aggregates in columns; nuclei and their processes; and supporting ependymal and neuroglial cells. It ends anteriorly in the brain and terminates below in a filament, the *filum terminale*, which is largely fibrous, with some coccygeal nerve strands. The cord occupies approximately the upper two-thirds of the neural canal. The latter, it will be recalled, results from the arched dorsal laminae of the vertebrae. Both cord and brain are covered by the three described meningeal layers. A dorsal and a ventral median fissure almost completely divide the cord into two symmetrical halves. Two enlargements appear, one in the cervical region associated with the roots of the brachial plexus; the other, the lumbar, associated with the spinal nerves of the lumbosacral plexus. Closely related to the dorsolateral surface, beginning in the fishes, are sensory ganglia derived from the neural crests. In *Amphioxus*, sensory cells lie in the cord; in cyclostomes they are partly in the cord and partly in the lateral sensory ganglia. In the classes above this level they lie outside the cord entirely.

The cord consists of gray and white substance (Fig. 134A). The gray is arranged in two upright crescents with their concavities directed laterally and joined at their middle by a commissure through which runs

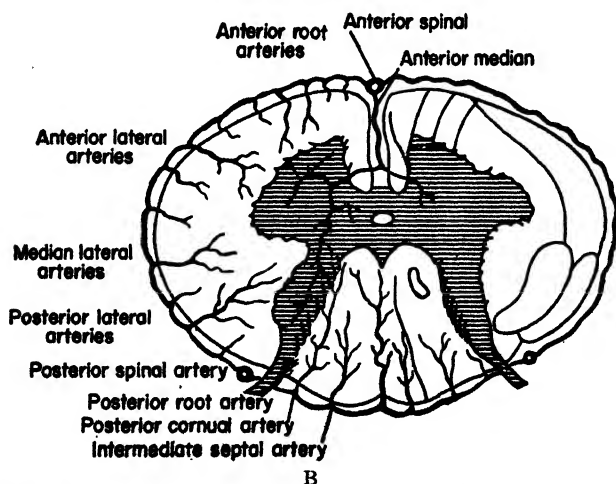
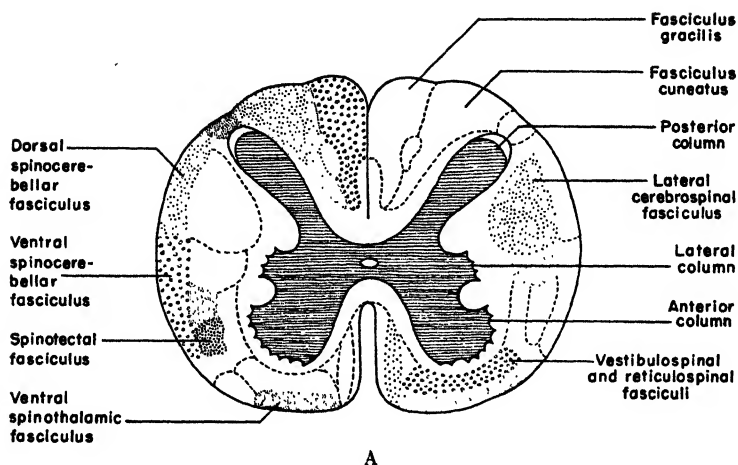


FIG. 134. *A*, cross-sectional view of human spinal cord. White, medullated nerve tracts surround the nonmedullated gray substance within the cord. *B*, blood supply to cord. Note that the arteries complete a circuit about the cord with anterior spinal and posterior spinal arteries extending vertically along the cord. (After Davis.)

the central canal. A horizontal plane cutting through the central canal would divide the crescents into right and left *dorsal* and right and left *ventral horns*, or columns. Each dorsal column includes the central processes of the dorsal sensory ganglia, which, as noted, lie outside the cord, and association cells with their processes, which lie within. Essentially the dorsal horn is the receptor and coordinating element. The two main nuclei are the *spongiosus* and *gelatinosus*; it also has several lesser cell groupings. The spongiosus forms the bulk of the body and neck of the dorsal column; the gelatinous fits on its top like a cap. Lesser nuclei include *Clarke's column*, or the dorsal nucleus; *dorsal* and *ventral cornucommissural nuclei* that relay impulses across the midline; and an *intermediate nucleus* at the junction of the dorsal and ventral columns.

The ventral column, or horn, is made up largely of motor neurons. Their many-branched dendrites connect with sensory or association axons; their axons are the ventral nerve roots. These unite with the dorsal sensory roots just outside the cord; together they form mixed spinal nerves. Motor nerve cells are arranged in a definite order in the ventral gray column; those to the trunk, for example, lie medially to those associated with the limbs.

The gray matter contains also a *lateral column*. This is a specialized cell mass at the junction of the anterior and posterior columns. The axons of these cells are myelinated and pass out with the ventral motor root as *preganglionic neurons* of the sympathetic nervous system. After emerging with the motor nerve roots these sympathetic nerve fibers separate from the segmental spinal nerves to enter the chain ganglia of the sympathetic nerve trunk, via the white rami communicantes.

White, or myelinated, nerve fibers surround the gray matter of the cord (Fig. 134B). The gray crescents incompletely separate these white areas into four bundles, or *funiculi*—a dorsal wedge-shaped one between the two dorsal horns, a ventral one between the two anterior horns, and a lateral division between the dorsal and ventral horns of each side. The dorsal and ventral bundles are further divided by the two median fissures into right and left dorsal and ventral funiculi. In this way three funiculi—a dorsal, a ventral and a lateral—are established in each half of the cord. In these funiculi the nerve fibers are arranged in definite ascending and descending fiber tracts. The ascending tracts include a medial *fasciculus gracilis* and a lateral *fasciculus cuneatus* in each dorsal bundle. The fasciculus gracilis contains fibers from the more caudally located spinal nerves, while the fasciculus cuneatus includes the more cranially located sensory nerve fibers. In a section of the cervical cord the fibers from the sacral area are the most medial, while

laterally those of the pelvic region, the back, and the neck appear in that order. In the fishes there is no white substance between the dorsal gray columns.

The ascending and descending tracts in the funiculi are named in accordance with their origin and their termination. Thus ascending tracts like spinocerebellar or spinothalamic have the spinal origin indicated first in their name, and the terminus in cerebellum or thalamus, second. Descending tracts, on the other hand, like vestibulospinal or cerebrospinal, which originate in the brain, are named in accordance with their origins, the brain origin preceding the terminus in the cord.

The lateral funiculus comprises in part the myelinated axons from the dorsal nucleus of the gray column. These ascending axons are the *dorsal* and *ventral spinocerebellar tracts* and unite the dorsal nucleus (Clarke's column) with the cerebellum. Other ascending tracts in both the lateral and ventral funiculi connect the cord with the thalamus and the midbrain. These *lateral* and *ventral spinothalamic tracts* extend to the diencephalon; the *spinotectal tract*, to the mesencephalon. Eventually, through neurons of the third order they reach the cerebral cortex. Impulses from the trunk and appendages traverse these pathways to reach higher cortical centers. The steps are these: Sensory spinal impulses pass to the cord; they are transmitted to the opposite side by commissure cells whose axons are the lateral and ventral tracts; these tracts ascend to diencephalon and midbrain, which in turn send tracts to the cerebrum.

The descending tracts lie mostly in the lateral and ventral fasciculi (Fig. 135). Functionally they unite brain and cord. Impulses from the brain traverse them to the motor cells of the ventral gray column. The nuclei of origin of these tracts lie in the brain. Most significant are the *anterior* and *lateral cerebrospinal fasciculi*, tracts which convey impulses from the cerebrum by way of the pyramids of the medulla to the motor cells of the ventral gray column. Other tracts include the *tectospinal* from the midbrain, conveying impulses of optical and acoustical origin to the cord; the *vestibulospinal* from the inner ear labyrinth to the cord; and the *rubrospinal* from the red nucleus of the midbrain to the cord, the latter apparently associated with righting movements of the body, at least in lower animals.

The descending motor tracts form the so-called *pyramid system*. The anterior and lateral cerebrospinal fasciculi, mentioned above, originate in giant pyramidal cells (cells of Betz) in the precentral, or *motor, gyrus* of the cerebral cortex. Their axons descend as the ventral and lateral cerebrospinal fasciculi, and together with the ventral-horn motor cells

they represent the so-called *motor system*. The giant pyramidal cells and their axons in the cerebrospinal fasciculi are the upper motor neurons; the anterior horn cells with their axons, the segmental motor nerve roots, are the lower motor neurons of this system.

From the above, the twofold function of the spinal cord becomes evident. It receives sensory impulses from the body and may resolve

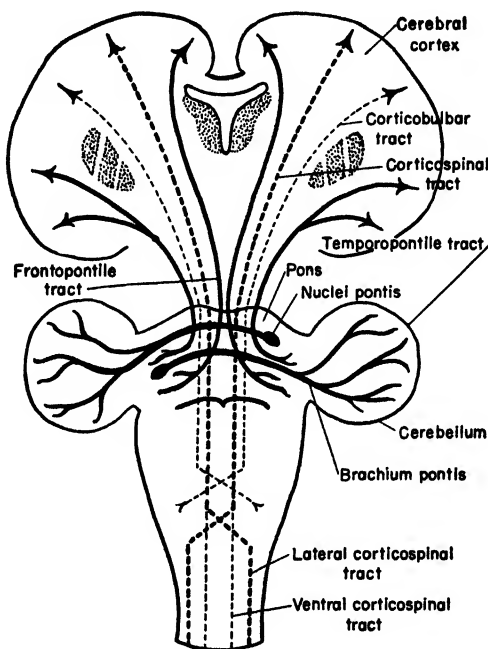


FIG. 135. Cerebral motor connections with remainder of the brain and with the cord. The cortex by its bulbar, pontile, and spinal tracts is in direct communication with, and in control of, the various parts of the striated muscular system. (Redrawn from Ranson and Clark.)

them directly by reflexes; it serves as the great highway mediating impulses between brain and body. In the rise of the vertebrates, independent functions of the cord are increasingly restricted concomitant with increasing numbers of connections between cord and brain. A reptile, for example, can carry out a number of muscular responses if the cord is severed, while in the mammal such injury leads to immediate profound disturbances involving loss of function and frequently to instant death.

THE SPINAL CORD IN THE CHORDATE CLASSES

Amphioxus shows several peculiarities of the spinal cord (Fig. 136). The dorsal and ventral roots of spinal nerves associated with the cord do not join as they do in mammals but run separate courses to the periphery. These roots leave the cord alternately so that the ventral pass

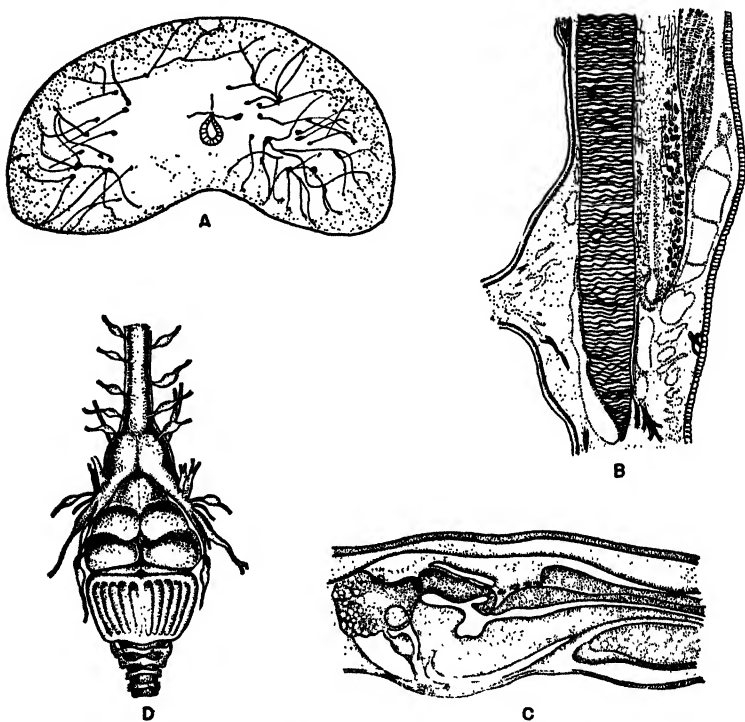


FIG. 136. A, *Amphioxus*, cross section of spinal cord. The substance of the cord is not yet arranged as it is in higher chordates. B, *Amphioxus*, sagittal section of brain. C, cyclostome, sagittal section of brain. D, cyclostome, dorsal view of brain, showing roots of cranial nerves and dorsal roots of sensory nerves as well as the peculiar telencephalon. (After Kükenthal.)

into the myotomes, while the dorsal pass between them. Nerve cells are absent in the posterior end, and only an ependymal sheath remains. Spinal ganglia are not segregated but occur within the dorsal roots and along the periphery of the dorsal nerves. Dorsal roots contain both sensory and visceral motor fibers. These fibers originate from cells

lateral to the ventral portion of the central canal. Giant ganglion cells lie in the cord near the entrance of the dorsal roots. Some of their axons decussate, *i.e.*, they pass both cephalad and caudad. According to Kappers, they form the early secondary sensory tract of the cord for vital sensibility. Ciliated neurosensory cells in the tentacles and the ocelli (simple eyes) along the cord are unique for *Amphioxus*. Glial or supporting cells appear only as primitive ependymal cells. A cord is absent in adult urochords and hemichords.

Cyclostomes. Cyclostomes exhibit the same alternate arrangement of dorsal and ventral nerve roots observed in *Amphioxus*. In *Petromyzon* the nerve roots are not joined; in the myxinooids they form a common mixed nerve. The cord is flattened dorsoventrally and is crescent-shaped when viewed in cross section, with the rounded tips of the crescent bent ventrally. The dorsal roots of the spinal nerves carry visceral afferent elements and visceral efferent fibers, in addition to the somatic. The bodies of some of these sensory cells arise in the cord, but most of them occur in extracordal ganglia. In the dorsal region of the cord the processes of these bipolar cells give rise to ascending and descending branches. The motor cell bodies in the lateral columns of the gray substance have processes which form a dendritic net in the margin of the cord, while some of them pass to the deeper portion of the gray matter and end in the region of Müller's fibers. Their axons are the ventral roots of the motor cells. Müller's fibers apparently form the motor system for the tail. They originate in the mid- and hindbrain and leave the cord by the ventral roots to terminate in the muscles. Numbering six to eight fibers, they extend along the medioventral aspect of the cord. The cyclostome cord is without an intrinsic blood supply but receives it from extracordal vessels.

Elasmobranch Fishes. In the elasmobranch fishes, dorsal and ventral gray columns first became differentiated. The dorsal are not separated into right and left moieties, as they are in mammals, but are segregated in a single mass. Ventral and dorsal nerve roots after leaving the cord join in the spinal nerves. Cell bodies of sensory fibers are associated in ganglia lateral to the cord. Visceral afferent fibers, together with the somatic, occur in the dorsal nerve roots, while visceral efferent and somatic efferent ones emerge together from the ventral nerve roots. Lumbar and cervical enlargements do not appear. In the anterior end of the cord the ventral roots are small or lacking. The occipitospinal nerves formed by these small ventral and larger dorsal roots at this level are the probable forerunners of the hypoglossal nerve of the tetrapods.

The ascending and descending tracts, constituting the white matter,

connect cord and spinal nerves with the posterior divisions of the brain. Descending tracts arising in the medulla oblongata are pathways for impulses from the brain to the body. Sympathetic chain ganglia are lacking but, at the junction of dorsal and ventral roots, visceral efferent branches, destined for the visceral tract, emerge.

Bony Fishes. Occipitospinal nerves are absent generally in bony fishes, and there is a consequent direct transition from cranial to spinal nerves. The caudal end of the cord, shortened in many species, with the root fibers of the lower spinal nerves occupying the caudal portion of the vertebral canal, resembles in this respect the mammalian cord. The dorsal gray matter has not yet separated into two horns, or columns. Somatic and visceral afferent fibers, as well as some visceral efferent fibers, comprise the dorsal nerve roots. Somatic afferent fibers originate partly in the cord and partly in extracordal ganglia, in contrast to the condition in the elasmobranchs. The ventral columns show no marked changes, compared with the cartilaginous fishes. Ascending and descending tracts are arranged in funiculi. The dorsal are small and are mainly descending tracts. Centers in the medulla oblongata from which descending tracts originate transmit impulses indirectly from the sense organs to the musculature.

White rami communicantes emerge at the junction of the dorsal and ventral spinal roots to enter the sympathetic nerve chain, marking the first appearance of chain ganglia in the vertebrate series.

Amphibia. Amphibia mark a transition from water to land life. Structurally there are well-defined differences between those which divorce themselves completely from the water and those which retain gills. The land amphibians metamorphose and experience two life histories—the larval and the adult. In the permanently tailed ones and in the larval stages of the Apoda, the cord resembles that of the elasmobranchs. There are many spinal nerves. In those which metamorphose only some 10 pairs are retained after metamorphosis. Cervical and lumbar enlargements occur, and sensory ganglia are segregated outside the cord. The gray substance is arranged in two crescents with a dorsal and a ventral column in each. The dorsal sensory processes pass into lateral and medial bundles of the white substance. Secondary sensory fibers also originate from the dorsal horns. They decussate in the ventral commissure and pass upward as spinobulbar and spino-mesencephalic fibers. The ventral-horn motor neurons send out axons which continue peripherally as ventral nerve roots. The white substance, in ascending and descending tracts, places the cord in communication with the brain. Rami communicantes from preganglionic cells at

the base of the dorsal gray horn extend to sympathetic chain ganglia, as they do in all higher vertebrates.

Reptiles. The reptilian cord, with some minor differences, is essentially similar to the mammalian. In the lizard *Sphenodon* and in the Crocodilia, with well-developed trunk and appendicular muscles, the gray ventral column is divided into a *medial* and a *lateral* group of *motor nuclei*. In the serpents, which are without limbs but with well-developed body muscles, the gray ventral horn is quite regular throughout, without cervical and lumbar enlargements. In the turtles, largely devoid of thoracic muscles but with well-developed limbs, the medial group of motor neurons, whose processes supply tail and neck muscles, are well developed, while the lateral exhibit cervical and lumbar enlargements. In the thoracic region this lateral group of cells thins out greatly. Throughout this class, development of the cord is coordinated with that of the appendages. Forming the ventral roots are *somatic* and *visceral motor fibers*, the former the motor divisions of the spinal nerves, the latter, visceral afferent fibers of white rami communicantes.

The dorsal roots contain *somatic* and *visceral afferent*, or sensory, *processes*. The cell bodies of these processes are grouped in *ganglia* lateral to the cord. Their fibers pass into a dorsomedial bundle in the white substance and in some species into ventrolateral bundles as well. Ascending tracts are definitely arranged; their nuclei lie in the fasciculus gracilis and cuneatus. From these nuclei tracts extend upward to the diencephalon and the cerebral cortex. Well-defined ascending *dorsal* and *ventral spinocerebellar*, *spinomesencephalic*, and *spinotectal tracts* place the body in communication with the midbrain and cerebellum. Descending white tracts arise in the medulla oblongata. These include a *vestibulospinal tract* from the vestibular nucleus and a *tectobulbar tract* from the optic tectum, all in synapse with reticular cells in the medulla. They reach the cord by descending *reticulospinal* paths.

Birds. Correlated with wing and leg development, the avian spinal cord shows corresponding cervical and lumbar enlargements (Fig. 137). Another peculiarity is the lumbosacral sinus, a widened space in the sacral cord probably correlated with the large sensory nerve roots in this region. It is filled with a glycogen-rich substance of vacuolated cells. The central canal continues through this area into the caudal region. Cell groups in the gray crescents are better defined than in the reptiles; they comprise *lateral*, *central*, *peripheral commissural*, and *dorsal nuclei*. External to the lateral funiculus, *marginal nuclei* probably represent displaced commissural and ventral horn cells.

In addition to the somatic afferent fibers, the dorsal roots contain the

special efferent fibers of von Lenhossék, together with delicate *visceral efferent fibers*. Most of the visceral efferent fibers leave by the ventral horn, however. Visceral and somatic sensory processes originate in spinal ganglia lateral to the cord. On reaching the cord, the axons

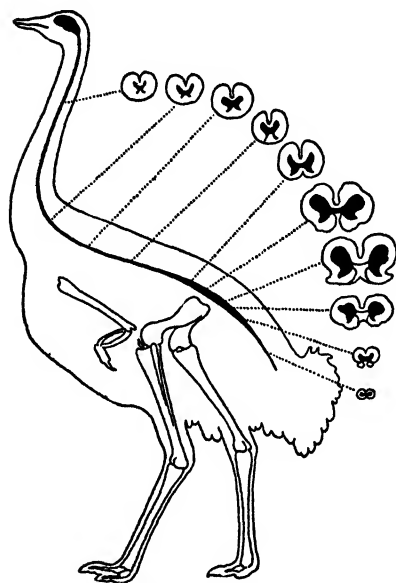


FIG. 137. The spinal cord of the ostrich, showing relative size at different levels. In flying birds, a similar expansion occurs at the thoracic level. (Redrawn from Edinger.)

of the spinal ganglion cells pass to the dorsal white funiculus and divide into ascending and descending branches. The dorsal funiculus is relatively small, owing to decreased skin sensibility. Impulses reach the mid-brain and cerebellum through well-defined tracts. These include the *spinomesencephalic*, which carries pain, temperature, and general tactile impulses; *spinobulbar* to the medulla oblongata; and *spino-cerebellar* to the cerebellum. This last tract traverses the length of the cord and indicates an increasing dependence of the cord upon the brain centers. Descending tracts, largely in the lateral marginal and in the ventral white area, include *cerebellospinal*, *vestibulospinal*, *tectospinal*, and *rubrospinal* tracts. These again point to the increasing influence of the

brain upon the cord and the activities of the body. The descending vestibular and cerebellar tracts are associated with balance; the tectospinal, which originates in the optic tectum, bespeaks the optic influence upon flight.

THE BRAIN

Correlated with the appearance of the neural tube is a rapid embryonic differentiation of the head. Special sense organs, with their outlets in the head and their inner connections at the anterior end of the neural tube, are laid down. This rostral end of the neural tube becomes the brain. In protochordates (Acrania) brain development does not pro-

ceed far in comparison with that in the Vertebrata (Craniata), as the names Acrania and Craniata imply. In the Acrania the neural canal widens into a brain ventricle; the walls of the neural tube, however, remain relatively thin and without any great proliferation of nerve cells and processes. A cluster of large ganglion cells proliferates in the roof of the neural tube of *Amphioxus*, just posterior to the brain vesicle proper. Since these cells are restricted to this area, they are considered a part of the brain. The brain vesicle of *Amphioxus* has been designated as the *archencephalon*; the ganglion cluster, the *deuterencephalon*. The notochord extends beneath this second brain vesicle. Anterior to the terminus of the notochord, the brain vesicle expands, and the original open end of the neural canal, called the *neuropore*, closes but leaves a slight outpocketing in the embryonic brain. With continued growth in higher forms a third division is differentiated between the primary vesicles. This is set off from the other two by transverse folds and is designated the *midbrain*. Thus early we recognize a forebrain, or *prosencephalon*; a midbrain, or *mesencephalon*; and a hindbrain, or *rhombencephalon*. *Commissures* of transverse nerve-fiber tracts further separate the three primary divisions. One, the anterior, is at the junction of pros- and mesencephalon in the dorsal brain wall; another, the cerebellar, is between mesencephalon and rhombencephalon. The prosencephalon undergoes further division into a *telencephalon* and a *diencephalon*, while the rhombencephalon differentiates into a *metencephalon* and *myelencephalon*.

With unequal growth of the various parts of the brain, flexures ensue. The first to appear is the *cephalic*, a ventral bend, at the level of the mesencephalon. A second, more caudal, the *cervical*, is also ventral; this is followed by a *dorsal pontine* flexure between the others. In birds and mammals the brain axis is almost at right angles with the axis of the cord. In lower forms the flexures are not prominent, and the brain is parallel with the long axis of the body.

The brain undergoes a variable thickening through proliferation of its nervous network, although some parts retain their primitive epithelial character. These changes are correlated with the functions of the five divisions. In the fishes the two anterior divisions are the olfactory centers. The midbrain is the center of sight; metencephalon and myelencephalon are the seat of the coordination of balance and for the lateral line system. Both metencephalon and cerebellum become great association centers.

The arrangement of white and gray matter is similar in the brain and spinal cord, with the addition, in the brain, of the gray cerebral cortex

over the white substance. The gray matter is centrally placed in proximity to the neural canal; the white is peripheral, with the exception noted above.

Beginning with the cyclostomes the five brain divisions indicated are well differentiated, and the somewhat detailed account given below

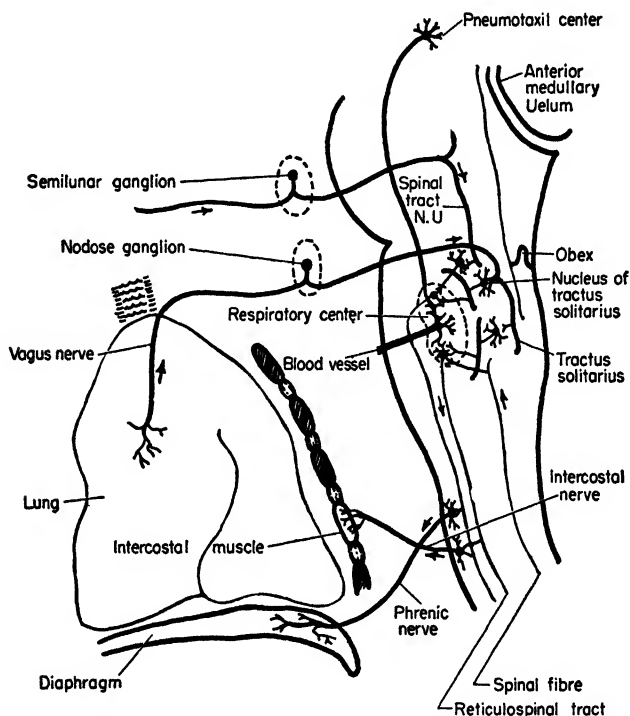


FIG. 138. The nervous mechanism that controls breathing. Vagal impulses pass from the lungs to the respiratory center of the medulla. Efferent impulses transmitted to the phrenic and the intercostal nerves regulate the action of the diaphragm and the intercostal muscles. (Redrawn from Ranson and Clark.)

attempts to summarize their significant structures and functions in mammals.

Myelencephalon (Medulla Oblongata). This fifth division of the brain is the focal point of important vital functions (Figs. 138, 139). It is a respiratory, vasomotor, and metabolic center which regulates the respiratory rate, blood pressure, and temperature. Destruction of the medulla brings about immediate death, since respiration ceases and the

blood vessels lose their tonus. On the other hand, if the brain is severed above the medulla, the animal may continue to breathe rhythmically and normal blood pressure may be maintained. The medulla is also the seat of the nuclei of the sixth to the twelfth cranial nerves, thus be-

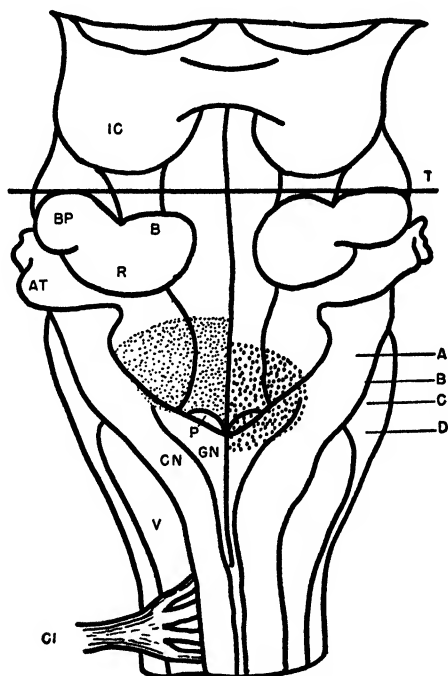


FIG. 139A. Dorsal view of brain stem of the cat after removal of cerebellum. The inspiratory subdivision of the respiratory center is projected on the right half on the floor of the right ventricle (dots); the expiratory subdivision on the left (stipple). Transection at line T, combined with bilateral section of the vagi, causes a continuous inspiratory spasm. AT, acoustic tubercle; B, brachium conjunctivum; BP, brachium pontis; Cl, first cervical root; CN, cuneate nucleus; GN, gracile nucleus; IC, inferior colliculus; P, area postrema; R, restiform body; V, tuberculum cinereum. (After Ranson and Clark.)

coming responsible for the wide range of activities expressed through this group of nerves. It marks the termination of certain ascending spinal tracts, and it is the relay center for transformation of stimuli, carried to this level by these tracts, and from here to higher centers of the brain. Through the *olivary body* on the floor of the medulla, sensations in the

locomotor system reach cerebellar centers and bring about coordination and balance. Through *Deiters' nucleus*, muscular movements of the head are correlated with those of the eye. The *reticular substance* is concerned in part with the translation of sensations of taste and smell into muscular movements involved in swallowing and in part with the

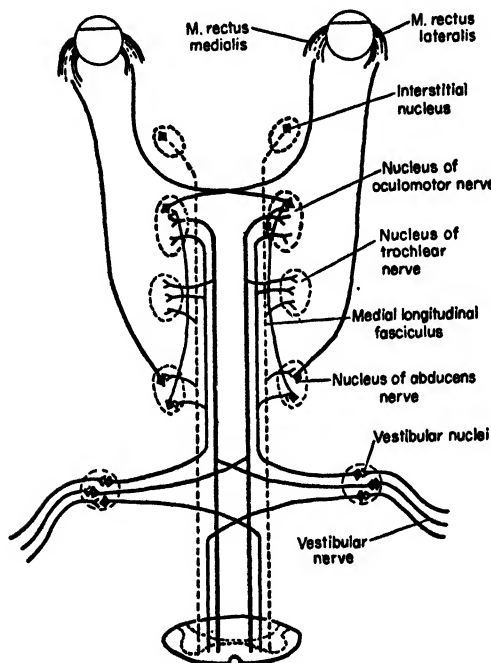


FIG. 139B. Nuclei of the medulla and mesencephalon. (After Ranson and Clark.)

transmission of impulses from the thalamus to the sympathetic nuclei of the cord.

As the hindmost division of the brain, the medulla merges posteriorly with the spinal cord; anteriorly it is continuous with the metencephalon. It extends from the rostral margin of the first spinal nerve root to the caudal margin of the pons. It widens cranially, while on its upper surface the neural canal likewise broadens to form the fourth ventricle. The roof of the ventricle is an epithelium, and its ependymal cells, together with the pia mater, form the *chorioid plexus*, which is the vascular tissue to this region. Externally the medulla is marked by a dorsal

and a ventral median fissure. Two lateral sulci, or furrows, one on each side and associated with emerging cranial nerves, further separate its surface into median, anterior, and posterior districts. Internally, in the open floor of the medulla, another furrow, the median sulcus, occurs in the floor of the fourth ventricle.

The following structures are included in the medulla:

1. Ascending and descending fiber tracts between the cord and higher brain levels
2. Nuclei associated with the abducens, facial, auditory, glossopharyngeal, vagus, accessory, and hypoglossal nerves
3. A reticular formation of gray matter and nerve fibers connecting the thalamus and the sympathetic nuclei of the cord

The tracts are continuations of those which have been described in reference to the cord. Among them are the *ventral* and the *lateral corticospinal tracts*. The first extends along either side of the median ventral fissure. The two ventral tracts enter the eminences on the ventral surface of the medulla, known as the *pyramids*. The lateral corticospinal tracts pass ventromedially from their lateral position in the cord. They decussate and join the ventral corticospinal tracts at the pyramids. Ventral and lateral corticospinal tracts originate from *giant pyramidal cells* in the motor cortex of the cerebrum. They leave this region as a single tract in each half of the brain. At the decussation of the pyramids about three-fourths of their fibers cross and become the lateral corticospinal tract, while the remaining fibers extend uncrossed along the ventral median fissure as the ventral corticospinal tract.

The motor nuclei mark the origins of several cranial nerves (Figs. 139B, 142A). These include the hypoglossal nucleus in the ventrolateral region, which extends upward to the fourth ventricle; the nucleus ambiguus, which is the somatic motor nucleus of the glossopharyngeal, the vagus, and the cranial portion of the accessory nerve; the nucleus salivatorius and nucleus lacrimalis, of uncertain function, in the upper part of the reticular substance; the dorsal nucleus of the vagus, lateral to the hypoglossal nucleus, whose axons pass to the smooth muscle and gland tissue supplied by the vagus; the nucleus of the vestibular nerve in the lateral wall of the fourth ventricle; and the two nuclei of the cochlear nerve.

The reticular substance is a mass of gray matter with interlaced nerve fibers occupying the central part of the medulla. The tract from the reticular substance continues to the thalamus, where it terminates in the reticular nucleus. As stated, it mediates impulses between the thalamus and sympathetic nuclei.

Associated with the medulla but lying external to it are the sensory ganglia of the following cranial nerves: the semilunar ganglion of the trigeminal nerve; the geniculate ganglion of the facial nerve; the superior and petrous ganglion of the glossopharyngeal nerve; the jugular and nodose ganglion of the vagus nerve; the spiral ganglion of the cochlear nerve; the vestibular ganglion of the vestibular nerve.

The medulla, in addition to its function as an intermediary for tracts between the brain and spinal cord and a nuclear center for certain of the cranial nerves, is, as noted, also a respiratory and vasomotor center. Vasomotor control is executed through afferent fibers in the glossopharyngeal and vagus nerves. The fibers of the glossopharyngeal nerve concerned with these functions originate in a slight bulbous enlargement (the carotid sinus) at the bifurcation of the carotid artery; the vagal fibers forming the depressor nerve pass from the aortic arch and aortic body. Both nerves extend to the medulla. When the blood pressure is increased beyond certain levels, this increase is communicated to the carotid and aortic walls. This stimulus is transmitted from the walls to the vasomotor center in the reticular substance of the medulla.

Respiratory control is chemical and depends upon carbon dioxide concentration in the blood. An increase in concentration affects the center in the reticular substance of the medulla and causes an increase in the respiratory rate.

The Pons. The pons, a relatively recent development, appears as a distinctive feature only in mammals with large cerebral hemispheres (Fig. 140A). It is a rostral continuation of the medulla, and its chief external characteristic and the one which gives it its name—pons, or bridge—is the band of transverse fibers on its ventral aspect. These fibers pass laterally from the medulla and continue into the cerebellum as the *brachium pontis*, or middle cerebellar peduncle. Internally the *nuclei pontis* are significant landmarks. They are cell clusters which connect the cerebrum with the cerebellum. The frontopontine tract passes from the cerebral cortex to the nuclei pontis. The axons of the cells of the nuclei pontis form the prominent transverse fibers that pass into the cerebellum. The trigeminal nerve, whose motor and main sensory nuclei are in the pons, emerges from the lateral border; abducent, facial, and auditory nerves emerge at its lower border. Other prominent features are the *pyramidal tracts* which traverse it laterally in their passage from the cerebral cortex to the spinal cord.

The Cerebellum (Metencephalon). The fourth division of the brain, the cerebellum, lies between the midbrain and the medulla (Fig. 140A, B). Its size varies. In birds and mammals, where balance and orienta-

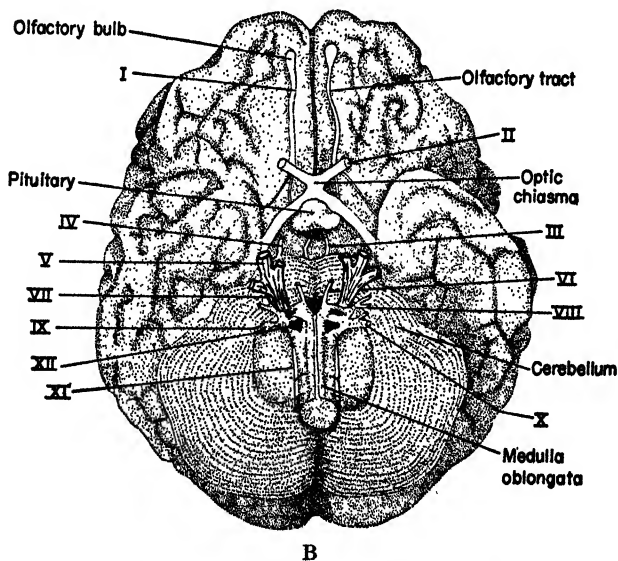
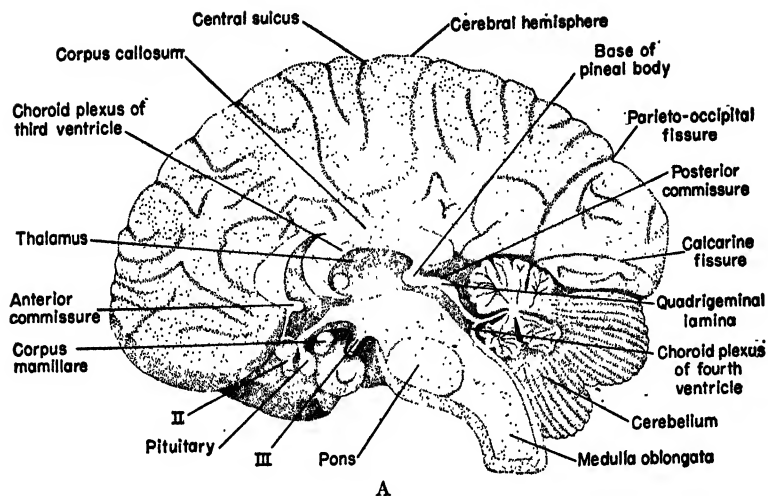


FIG. 140. *A*, sagittal section of the human brain; *B*, ventral view of the human brain, showing cranial nerve roots.

tion depend almost entirely upon muscular activity and coordination, it is relatively large; in amphibians and reptiles, where the body is in relatively close contact with the earth, it is less developed.

The cerebellum of man is divided into *anterior*, *posterior*, and *median lobes*. The anterior and posterior represent the original vestibular and spinal elements or connections, while the middle is associated with the cerebral tracts. Their external division is obscured by an expansion of the middle lobe, or neocerebellum, that has become associated with the cerebrum through the transverse fibers of the pons and the brachium pontis. The anterior lobe remains associated with the balancing mechanism of the ear, while the posterior, also called the flocculonodular lobe, consists of a middle nodulus with a body of myelinated fibers extending laterally, also associated with the ear and with ascending spinal tracts.

Prominent features of the mammalian cerebellum are the two *lateral hemispheres* with the *vermis* between them. These hemispheres include both anterior and middle lobe substance.

Internally the cerebellum is made up of an inner compact *white mass* and an outer *gray substance*, the cerebellar cortex. The white mass extends toward the cortex in a series of ramifications, giving this region a tree-like appearance, called the *arbor vitae*. In the central white core is a gray island, open on its medial side, the *dentate nucleus*. Other nuclei in this area are the *emboliform*, the *globose*, and the *fastigii*. Axons of the Purkinje cells terminate in these subcortical nuclei, and efferent pathways from the cerebellum continue from these centers by new neurons.

The cerebellum is associated with the spinal cord and the brain stem through afferent and efferent fibers in the *superior*, *middle*, and *inferior peduncles*. The superior peduncles connect it with the midbrain and the thalamus; the middle, also called the brachium pontis, with the pons; the inferior, with the medulla oblongata and the spinal cord.

The superior peduncle, or brachium conjunctivum, arises from the nuclei in the white substance of the cerebellum, as indicated. The fibers are efferent and pass to the red nucleus and the thalamus of the opposite side.

To understand the nature of the middle peduncle it is necessary to trace the origins of its fibers. It will be recalled that corticopontine fibers originate in the cerebral cortex and terminate in the nuclei pontis. From these nuclei transverse fibers enter the cerebellum on the opposite side. This large, compact bundle of transverse fibers extends into the cerebellar hemispheres as the middle peduncle.

The inferior peduncle, also called the restiform body, consists of afferent fibers to the cerebellum. Its several tracts include the posterior spinocerebellar tract, which terminates in the vermis; the olivocerebellar tract, which arises in the olivary and accessory olivary nuclei; arcuate fibers from the arcuate nuclei; and fibers from the accessory cuneate nucleus.

The gray substance, exclusive of that found in the nuclei in the interior of the cerebellum, forms the cortex. Because of the laminations in the white substance, which are covered by the gray, the cerebellum in section has a foliated appearance.

In detail, the cortex has an outer *molecular* and an inner *nuclear* or *granular layer*, between which is a single layer of *Purkinje cells*, peculiar to the cerebellum.

The molecular layer contains characteristic basket cells, stellate neurons, dendrons of Purkinje cells, and axons and their branches from the underlying granule cells.

The granular cells give off four or five dendrites each, which terminate in small, claw-like endings in contact with adjacent granule cells and are a part of the afferent system to the Purkinje cells. The axons of the granular cells pass into the molecular layer and presumably enter into synapses with the Purkinje cells, while axons of the latter pass through the granular layer and into the cerebellar nuclei. They represent the first step in the efferent relay from the cerebellum.

The cerebellum receives afferent fibers from the spinal cord and the medulla, cerebral by way of the pons, and fibers from the labyrinth of the ear. Afferent impulses are conveyed to the distinctive Purkinje cells of the cerebellum. These cells, characterized by greatly branched dendritic processes, accept impulses from the sources indicated. Their axons pass to the medulla. From the medulla secondary neurons continue to the anterior gray horns of the cord, placing the cerebellum in direct communication with the motor roots of the spinal nerves. The functions of pons and cerebellum relate to coordination of muscular movements. In land vertebrates, afferent impulses (proprioceptive) pass from the joints to the cerebellum, and postural *tonus* is maintained by efferent impulses originating in the cerebellum. These proprioceptive impulses are not to be confused with those which originate in the inner ear. Proprioceptive functions become associated with the cerebellum upon the appearance of spinocerebellar tracts, while the inner ear connections with the cerebellum represent the original mechanism for maintaining balance in the vertebrates.

The cerebellum originally was the center concerned entirely with

equilibration. Its primary connections were with the terminal nucleus of the vestibular nerve of the ear. The auricular lobes of the cerebellum first appear in fishes and are associated with the vestibular nucleus and lateral line system. This auricular extension persists as the flocculus in the posterior cerebellar lobe in higher animals. In addition, the mammalian cerebrum exerts a controlling influence on the cerebellum, through tracts from the cerebrum to the pons and from the nucleus pontis to the cerebellum. This results in the formation of the neocerebellum.

Midbrain (Mesencephalon). The midbrain, or mesencephalon, consists of a *dorsal tectum*, the corpora quadrigemina, known also as the superior and inferior colliculi, and a ventral part, the *two cerebral peduncles* (Fig. 140). It also connects the cerebrum with the pons and the cerebellum. The *cerebral aqueduct*, a narrow canal, traverses its floor and unites the third and fourth ventricles.

Internally the midbrain comprises a *central gray mass* around the aqueduct; the corpora quadrigemina in the dorsal portion; the tegmentum in the middle area; and the peduncles in the lower portion of the section. The aqueduct, about $\frac{3}{4}$ in. long in man, is lined with ependymal epithelium. Immediately around this is the gray matter, in which the nuclei of the oculomotor, trochlear, and mesencephalic root of the trigeminal nerve are differentiated.

The *tegmentum*, a continuation of the dorsal part of the pons, consists of longitudinal and transverse fibers with interspersed gray matter. Of the tegmental nuclei situated in this region, the most prominent is the red nucleus. This is a center through which the cerebellum acts on the motor functions of the medulla and the cord.

Fibers from the superior peduncle of the cerebellum decussate in the tegmentum, and these crossed fibers enter the red nucleus in part and in part ascend to the thalamus. These fibers arise in the dentate nucleus of the cerebellum. In the red nucleus originates the rubrospinal tract, which passes into the spinal cord.

The corpora quadrigemina constitute the roof of the midbrain. As the name indicates, there are four corpora. The inferior, largely of gray substance, are known as the nuclei of the inferior colliculi. The inferior quadrigemina become associated with cochlear, or auditory, functions. The superior are composed of superficial white layers and more deeply placed gray ones. Below these are the optic and lemniscus strata in that order. Optic fibers terminate in the optic and gray layers. The lemniscus contains spinotectal fibers from the spinal cord and corticotectal fibers from the cerebrum. The superior bodies are the centers for sight and coordination of the eye muscles.

The midbrain is one of the centers for postural reflexes. Together midbrain, corpus striatum, medulla, and upper portions of the cord apparently can function independently of the cerebellum in maintaining postural tonus. Severance of the midbrain between the superior and inferior colliculi results in decerebrate rigidity, which means that the animal may maintain a fixed posture for long periods when placed in various positions. If the brain is sectioned anterior to the midbrain, such rigidity does not occur. The superior colliculi, it will be recalled, are optic, the inferior auditory, centers. Impulses from these centers are relayed to the occipital cortex of the cerebrum and thus reach conscious levels.

The Diencephalon. The diencephalon is the second division of the brain (Fig. 140). It surrounds the third ventricle, which is constricted in reptiles, birds, and mammals because of the thickening of the lateral walls of the diencephalon. These walls constitute the thalamus. The region is largely an intermediary between the cerebral centers and the lower divisions of the brain and spinal cord; it is also a terminus for ascending spinal tracts. In the amniotes many optic fibers end in the thalamus. Besides its function as a relay center, the diencephalon is the seat of the parietal organ and the epiphysis from the roof of the third ventricle and the hypophysis from the floor. The latter has significant endocrine functions, while the parietal organ is developed into a dorsal eye in the lizard *Sphenodon*. The epiphysis, or pineal gland, also has had endocrine functions ascribed to it.

An *epithalamus*, *thalamus*, and *hypothalamus* are differentiated in the diencephalon. In addition, a *metathalamus* and *subthalamus* may be designated. The thalamus is the chief structure and, as indicated, constitutes the walls of the diencephalon. Its posterior portion is widened, while the anterior is tapered, with right and left halves approximating each other, forming a definite commissure at the point of meeting of the two halves in certain reptiles and in the mammals. It is predominantly gray matter subdivided into a number of nuclei. Walker has designated some 27 in this area, associated with the relaying of impulses. He separates them into *midline*, *anterior*, *medial*, *lateral*, and *posterior nuclei*.

Nuclei of the midline group are associated with the hypothalamus. They do not make cortical connections and are probably concerned with visceral sensibility. Those of the anterior group receive fibers from the mammillary body and send others to the cerebral cortex. The medial group receives connections from the lateral and from the basal olfactory areas. They are a relay path between cerebrum and cerebellum. The lateral and posterior nuclei receive fibers from other thalamic

nuclei and from the geniculate bodies. They connect with the parietal and temporal lobes of the cortex and apparently function in visual and auditory integration. They also receive fibers from the cochlear nuclei by the lateral lemniscus, whose fibers extend to the auditory area of the cerebral cortex.

Two geniculate bodies, a medial and a lateral, occur on each side. They are also called the metathalamus. Right and left medial bodies connect with each other by a commissure through the posterior part of the optic chiasma. Their fibers terminate in the temporal area of the cerebral cortex. The lateral geniculate bodies mark the termination of the optic tract. Axon fibers from these nuclei end in the cortical area surrounding the calcarine fissure in the posterior lobe of the cerebrum.

The subthalamus between the dorsal thalamus and the tegmentum of the midbrain is a link between the basal nuclei of the forebrain and the tegmentum of the mesencephalon.

The epithalamus lies in the roof of the third ventricle. It includes the *pineal body*, the *habenular commissure*, the *stria habenularis*, and the *habenular trigone*. The pineal body extends upward for several millimeters from the roof of the ventricle, from which it emerges by a hollow stalk. Its neuroglial cells are surrounded by a vascular plexus; the cells are assumed to have endocrine functions. The habenular nucleus is an olfactory correlation center receiving fibers from the stria medullaris, which is made up in part of fibers from the basal olfactory areas. From the habenular nucleus a habenulopeduncular tract passes down to the interpeduncular ganglia on both sides to form reflex olfactory pathways.

The hypothalamus, a complex structure on the floor of the third ventricle, consists of *mammillary bodies*, the *tuber cinereum*, the *infundibulum*, the *hypophysis*, and *optic chiasma*, with both afferent and efferent fibers. Among the afferent tracts is the *medial forebrain bundle* arising from nuclei in the olfactory cortex. It distributes its fibers in part to the hypothalamus and to the tegmentum of the midbrain. Descending hypothalamic fibers extend to the brain stem. Efferent fibers include those from the nucleus supraopticus and nucleus paraventriculus. These efferent tracts are called the *supraopticohypophyseal* and the *paraventriculohypophyseal tracts*, respectively. They pass to the neural lobe of the hypophysis and presumably are associated with posterior pituitary lobe functions. Their severance causes excessive diuresis. From the hypothalamic nuclei descending fibers also pass to the midbrain.

The *stalk* of the hypophysis extends downward to join the neural lobe. The cavity within the stalk, the *infundibulum*, represents an extension

of the third ventricle. The stalk is attached to the tuber cinereum, a small gray body between the mammillary bodies and the optic chiasma. The hypophysis has two lobes: the *posterior*, neural in origin, of neuroglial cells called pituicytes; the *anterior*, which joins the posterior during embryonic development and is derived from the pharyngeal epithelium in the roof of the embryonic mouth. An *intermediate lobe* is associated with the infundibular stalk. These lobes will be described in connection with their endocrine functions.

The optic tracts are continuations of the optic nerves. At the optic chiasma they terminate for the most part in the *lateral geniculate ganglia*. A few fibers pass to the superior colliculus of the corpora quadrigemina and to the pretectal region. From the lateral geniculate bodies, other fibers arise as optic radiations to the visual center in the occipital cortex.

The hypothalamus is an ancient center for the "excitation and integration of visceral and somatic responses which regularly form a part of the reaction pattern of fear and rage."¹ Ranson states that electrical stimulation of the hypothalamus causes increased rate and depth of breathing, a rise in the arterial blood pressure, pupillary dilatation, struggling, and muscular activity, all evidence of emotional excitement. Lesions may cause somnolence, disturbed temperature regulation, diabetes insipidus, and disturbances of fat metabolism.

Telencephalon. The telencephalon includes the *rhinencephalon*, or olfactory lobe, the *corpus striatum*, or "primitive efferent system of the brain," and the neopallium, or *cerebral cortex*.

The rhinencephalon, concerned with olfaction and with the transmission of the sensation of smell, in fish and reptiles includes most of the forebrain (Figs. 143, 144). In mammals it shows a variable development. Thus in the rodents, ungulates, and carnivores it is highly developed (macrosmatic); in man it is reduced to such an extent that it lies on the undersurface of the cerebrum (microsmatic). In the Cetacea it is vestigial or absent.

The rhinencephalon includes a bundle of *olfactory nerves* of which the sensory termini are in the organ of smell, an *olfactory bulb* which in mammals rests upon the cribriform plate of the skull, and an *olfactory tract* which unites the bulb with the brain. This tract lies in the olfactory sulcus on the inferior surface of the frontal cerebral lobe. *Mitral cells* and *tufted cells* constitute the bulb. They are in synapse with the olfactory nerves. Their axons form the olfactory tract, which passes to

¹ Bard, 1934, after W. S. Ranson, *The Anatomy of the Nervous System*, p. 231. W. B. Saunders Company, Philadelphia, 1943.

the uncus, a hook-shaped portion of the temporal lobe. This region of gray substance, because of its pear-like shape, is known in lower animals as the pyriform area. The olfactory nerves are the primary neurons; the lateral olfactory tracts form secondary neurons. The tertiary neurons arise in the pyriform area and pass medially to the pallium. Nerve cells at the medial margin of the pallium receive the olfactory impulses from the tertiary neurons. This group of nerve cell bodies constitutes the *dentate nucleus*. Their axons pass into the adjacent pallium and form the *hippocampus*. Here olfactory sensations are coordinated with other sense impressions.

From the hippocampus a system of transverse fibers, known as the *fornix*, pass to the hippocampus of the opposite side and to the hypothalamus. In addition, *commissural fibers* also join the two hippocampi.

To summarize these pathways: Olfactory impulses pass from the primary neurons in the nasal epithelium to the glomeruli on the floor of the cribriform plate. Here they are taken up by the mitral cells, whose axons, the lateral olfactory tracts, or striae, convey the impulses to the pyriform area. From this region they are transmitted to the hippocampus and dentate fascia, thence to the hippocampus of the opposite side, to the thalamus, and the reticular substance of the medulla. Some end in the mammillary bodies. Beyond the hippocampus lies the cerebral cortex, or the neopallium.

The Corpus Striatum. In each cerebral hemisphere, a gray mass of tertiary neurons of the olfactory chain encroaches on the corresponding ventricle as a basal ganglion, or *corpus striatum* (motor). In mammals, two additional nuclei, the *caudate* and *lentiform*, associated with underlying olfactory areas as well as with the cerebral cortex, are added to the corpus striatum. They are separated by a band of white fibers, the *internal capsule*. These fibers unite the optic thalamus with the cerebral pallium. It will be recalled that the pyramidal system places the medulla and the spinal cord under control of the cerebrum. Antedating this system phylogenetically is the extrapyramidal system, or corpus striatum, primarily connected with the olfactory fibers, and in part an olfactory reflex center. In reptiles and birds it pushes into the lateral ventricle, while in mammals it is overshadowed by the neopallium. It is connected not only to the olfactory neurons but to the cortex, subthalamus, and mesencephalon. Included in the extrapyramidal system are the subthalamic nucleus, the substantia nigra, and the red and the olivary nuclei. These nuclei regulate in part many of the visceral and automatic activities. Apparently the system also plays a role in the regulation of tonus of the striated musculature; the

corpus striatum furthermore appears to be one of the heat-regulating centers in warm-blooded animals.

The Cerebral Hemispheres. In man the cerebrum is divided into two hemispheres that overshadow the remainder of the brain to such an extent that only from a basilar or posterior view do the remaining parts come into evidence (Fig. 140). The cortex may be separated into *frontal, parietal, temporal, and occipital lobes*. A *central sulcus* (fissure of Rolando) divides the frontal from the parietal lobes. A *lateral cerebral fissure* (fissure of Sylvius) separates the temporal from the parietal lobe, while the *parietooccipital fissure* demarcates the parietal from the occipital lobes. Another part that has become overgrown and hidden at the bottom of the lateral fissure is the *insula*. The areas between the several fissures are raised into gyri, or convolutions. The fissures between gyri are sulci. Between the two hemispheres at the bottom of the median longitudinal fissure, the corpus callosum unites the two cerebral halves.

Internally, the cerebrum exhibits an outer gray cortex, which follows the fissures and covers the convolutions unevenly, and an inner white medulla. The corpus callosum, already mentioned, joins the two hemispheres and forms a heavy band of transverse fibers, spread out laterally into the hemispheres as the radiation of the corpus callosum. The *lateral ventricles* underneath the corpus callosum are the cavities of the cerebral hemispheres. Each has an anterior, posterior, and inferior horn and a central portion. The *chorioid plexus*, over the central part and the inferior horns, is continuous with that of the third ventricle. The lateral ventricle communicates with the third ventricle through the *interventricular foramen*. The third ventricle in turn connects with the fourth through the *cerebral aqueduct*. The lateral ventricle is lined with *ependymal cells*, just as are the remaining cavities.

The Neopallium. The term pallium (mantle) designates the gray cortical layer of the cerebral hemispheres (Fig. 141). Originally it was largely an olfactory center. In mammals, other sensory centers appear. The pallium has six layers, each with distinctive features: (1) an outer laminar; (2) an external granular; (3) a pyramidal; (4) an inner granular; (5) a ganglionic; (6) a multiform layer.

Various types of sensory impulses, including auditory, visual, and tactile, are transmitted to the corresponding sensory areas of the cortex. These areas lie posterior to the central sulcus. The visual area, for example, lies in the occipital lobe, the acoustic area in the temporal lobe, other sensations in the parietal lobes. The motor area of the cortex, just anterior to the central sulcus, is the center for the initiation

of voluntary motor impulses. These originate in specialized cells called Betz cells and are transmitted by the pyramidal tract. Association areas, constituting another portion of the cortex, are formed by short intracortical association and subcortical fibers, the latter underlying the gray substance and the long association bundles. They unite various parts of one hemisphere, while the commissural fibers join the two hemispheres.

Certain sensory tracts conveying proprioceptive impulses ascend the cord to end in the nucleus cuneatus and gracilis of the medulla. From here arcuate fibers decussate and continue upward in the medial lem-

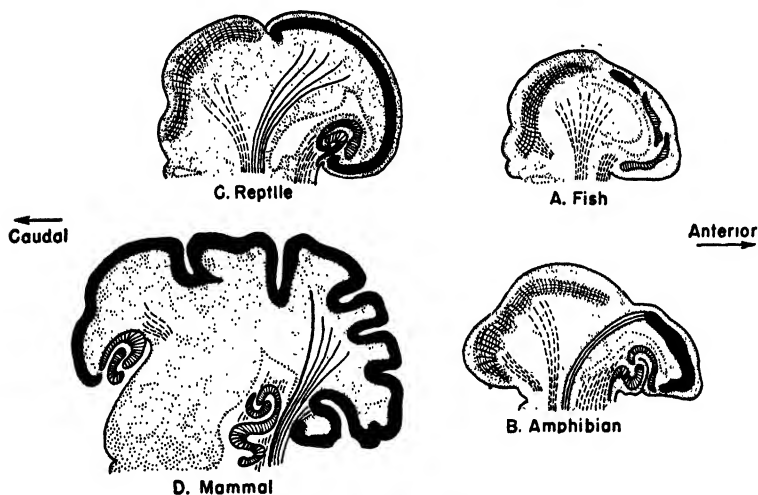


FIG. 141. Evolution of neopallium. Heavy black lines indicate the neopallium. (Redrawn from Edinger.)

niscus to terminate in the ventral thalamic nucleus. From this nucleus fibers pass in the internal capsule to the cortex. Other fibers conveying touch, pain, and temperature sensations form the spinothalamic tract, which decussates and ascends along the cord to the central nucleus. They proceed from this center to the postcentral gyrus of the cerebral cortex. Still other fibers from the nuclei of the trigeminal, facial, glossopharyngeal, and vagus nerves join the tract to the thalamus and from the thalamus pass secondarily to the cerebrum.

Afferent and Efferent Cerebral System. Two great systems, the afferent and the efferent, relate the cerebrum to the body and enable the cortex to act as executive in the regulation of motor activity.

The afferent system conveys sensations from muscles, articulations, and organs within the body and sensations from outside the body through special sense organs and sensory endings in the integument. Sensations of the first type are *interoceptive* if they come from the organs of the body and *proprioceptive* if they originate in the muscles and joints. Sensations from without are called *exteroceptive*. Interoceptive and proprioceptive sensations with few exceptions terminate in the cerebellum, while exteroceptive sensations are conveyed to the cerebral cortex. Here complex correlations and integrations occur. Thus tactile sensations may be correlated with auditory and visual. Other correlations and integrations go on constantly, bringing such sensations to a conscious level.

The tracts which convey impulses from the sensory nerves and through the cord to the brain are well established. Impulses of this type are carried in the posterior and anterior funiculi of the cord. It should be noted that tactile, pain, and temperature fibers have a constant position in these ascending tracts. Impulses conveyed in this manner reach the thalamus by way of the nucleus cuneatus and the nucleus gracilis; some of the fibers in the tracts terminate in the gray matter of the cord and from there pass to the thalamus. From the thalamus they reach the sensory areas posterior to the central sulcus of the cerebrum.

Sight and hearing have their own distinctive cortical centers. The center for the former is in the posterior cerebral lobe; that for the latter, in the transverse gyrus of the temporal lobe.

The efferent pathways originate in the cells of the motor center of the cerebrum rostral to the central sulcus. They form the motor mechanism or tract from the cortex to the spinal cord (Fig. 142). This begins with upper motor neurons and their fibers in the cortex. The fibers pass to both cranial and spinal motor nerve roots. The cells of these motor nerve nuclei in the spinal cord and their axons to the muscles are the lower motor neurons. They descend the cord by the corticospinal, or pyramidal, tract, which divides into the lateral cerebrospinal tract in the lateral white column of the cord, encountered in the description of the ventral cerebrospinal tract in the anterior white column. In addition to these tracts, which have their outflow in the motor roots of spinal nerves, definite motor pathways exist for the cranial nerves. The elements involved in these tracts are the *giant pyramidal cells* in the motor cortex and their axons, the *corticobulbar fibers*, extending to the lower motor neurons of the brain stem. These motor neurons are the nuclei of the oculomotor, trochlear, trigeminal, abducent, facial, glossopharyngeal, vagus, accessory, and hypoglossal nerves.

Other motor pathways, known as the extrapyramidal tracts, are the

corticopontocerebellar and the *cerebellorubrospinal* pathways. The corticopontocerebellar places the cerebellum in connection and under partial control of the cerebrum, while the cerebellorubrospinal enables the cerebellum to control muscular tone and muscular coordination.

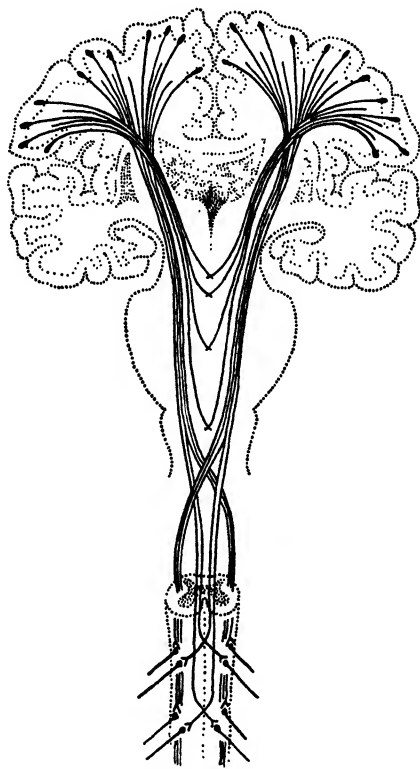


FIG. 142. Motor system of cerebral cortex. Direct and crossed cerebrospinal tracts take origin in the motor cortex and descend to varying levels before they pass as motor nerves from the ventral horns of the cord. (Redrawn from Gray.)

THE PERIPHERAL NERVOUS SYSTEM

The peripheral nervous system includes the cranial and spinal nerves and the autonomic nervous system (Figs. 145, 146, 147). These elements stand in close functional relationship with the central system, the brain and spinal cord. Both structurally and functionally the peripheral system is an extension of the central nervous system. The central

system is the great coordinating and integrating center of the body; the peripheral makes the animal aware of the world, within and without, through its sensory components and produces action, both within and without, through its motor elements. Awareness as employed here does not necessarily imply consciousness, since many impulses reach the cord and the brain without exciting the conscious centers; yet they cause the central system to respond to changes in the internal or external environment. Because of their varied functions and locations it is convenient to distinguish between cranial and spinal nerves. Because of its visceral functions and its distribution, we separate the autonomic nervous system from the other elements.

The Cranial Nerves. There are 12 pairs of cranial nerves in reptiles, birds, and mammals. In the cyclostomes, fishes, and amphibians there are 10 pairs. The eleventh and twelfth in the higher forms have developed from the first two spinal nerves, which have become incorporated with the cranial system. In *Amphioxus*, 2 pairs of sensory cerebral nerves arise from the brain, and some 60 pairs are associated with the spinal cord. Attempts have been made to homologize the first few spinal nerves of *Amphioxus* with the trigeminal, facial, glossopharyngeal, and vagus nerves of the vertebrates, but no conclusive evidence has been presented that makes this homology entirely plausible. In *Amphioxus* the spinal nerves are segmentally arranged; the sensory and the motor nerves do not join as they emerge from the cord, as they do in the vertebrates, but remain separate. The dorsal nerves are mixed, *i.e.*, they contain both sensory and motor fibers, while the ventral are purely motor.

The cranial nerves in the vertebrates are associated with the various divisions of the brain (Figs. 140, 143, 144). They emerge from the brain case through foramina and are distributed chiefly to the head and neck. Vagus and accessory nerves, however, have a wider distribution; the former supplies the digestive tract, heart, and lungs, in addition to branches in the head and neck, while the accessory has a spinal component to the trapezius muscle of the shoulder.

The cell clusters that mark the origins of the motor nerves or near which the sensory nerves terminate in the brain are known as the nuclei of origin and of termination, respectively. These deep centers have been considered in connection with the description of the brain. In addition to such nuclei, the sensory cranial nerves are immediately associated with ganglia outside the brain, homologous with spinal sensory ganglia.

We distinguish somatic and visceral tissues in the body. The former

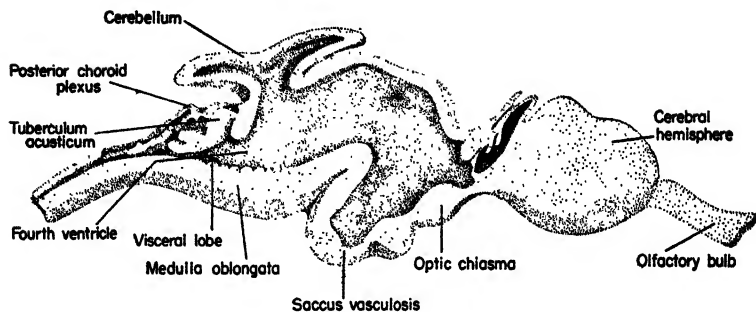


FIG. 143A. Sagittal section of dogfish brain.

O, Terminal nerve

I, Olfactory nerve

II, Optic nerve

III, Oculomotor nerve

IV, Trochlear nerve

V, Trigeminal nerve

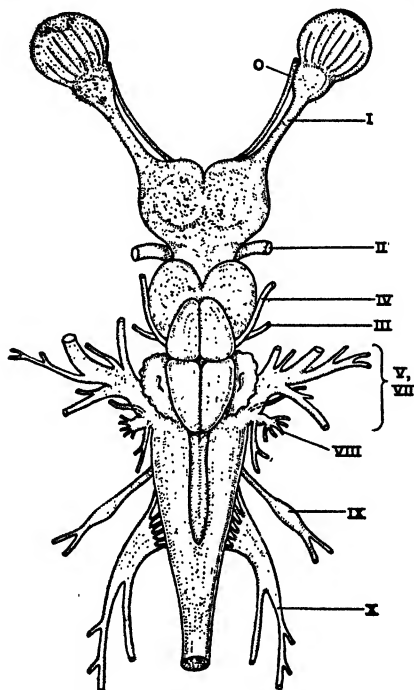


FIG. 143B. Dorsal view of dogfish brain.

VI, Abducens nerve

VII, Facial nerve

VIII, Auditory nerve

IX, Glossopharyngeal nerve

X, Vagus nerve.



FIG. 144A. 1, 2, 3, 4, 5, early developmental stages of the heart correlated with the growth of the vagus nerve; 6, lateral view of the tadpole brain, cranial nerve-root ganglia 5-10, and vagal connections to the heart; R.H., olfactory lobe; Hh., cerebral hemisphere; Mh., midbrain; Nh., medulla oblongata; V, trigeminal ganglion; VII, geniculate ganglion; VIII, acoustic ganglion; X, vagal ganglion. (Redrawn from His.)

comprise the limbs and body wall; the latter, the soft parts, organs, intestinal tracts, etc. These parts are supplied by somatic and visceral nerves, respectively. Gills and their musculature are visceral in origin.

In the evolution of the muscles and tissues derived from these arches, the nerves that were originally visceral have been retained with some modifications.

The following designations, applied to the cranial nerves and their relations to visceral or somatic organs, is suggested by Herrick:

Sensory Nerve Types

1. General somatic afferent (sensory from the skin)
2. Special somatic afferent (vestibule and cochlea of ear)
3. General visceral afferent (from mucous membranes of visceral origin)
4. Special visceral afferent (from taste buds)

Motor Nerve Types

1. General somatic efferent (to skeletal muscle)
2. Special visceral efferent (to muscles of visceral origin)
3. General visceral efferent (to smooth muscles)

Under a more general classification, cranial nerves I, II, VIII are somatic afferent; III, IV, VI, XII are somatic efferent; V, VII, IX, X, XI are somatic and visceral afferent and efferent.

It will be recalled that the developing neural cord consists of a dorsal alar sensory and a basal motor plate, separated by a sulcus limitans. In the alar plate a *somatic sensory column* is developed at

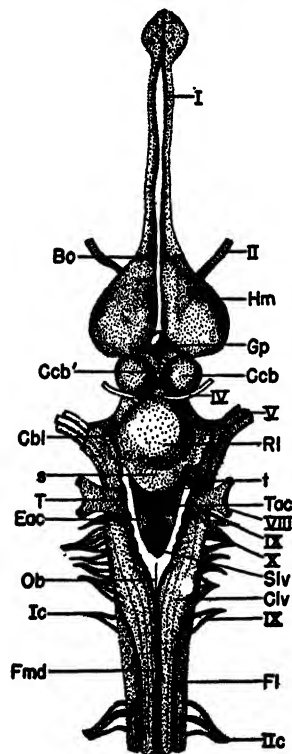


FIG. 144B. Dorsal view of alligator brain, roman numerals corresponding to cranial nerves; Hm, telencephalon; Gcb, midbrain; RI, cerebellum; Tac, fourth ventricle. (Redrawn from Bronn.)

the level of the future medulla oblongata near the margins of the fourth ventricle. Below this is a *visceral sensory column*, also in the alar plate. In the basal plate the *visceral motor column* occurs just below the sulcus limitans, and the *somatic motor column* lies ventral to it.

The nuclei which mark the termination of sensory nerves lie above the sulcus limitans; those which mark the origins of motor nerves lie below it.

The somatic afferent nuclei of this area are subdivided into a general somatic afferent group, which receives sensory fibers from the skin, and a special somatic afferent group, which receives the sensory fibers of the acoustic nerve, and in the fishes the lateral line system.

The visceral afferent column in the medulla receives general and special afferent fibers, as indicated, from the facial, glossopharyngeal, and vagus nerves. These fibers terminate in the nucleus solitarius of the medulla.

The visceral motor column contains a ventrolateral group of nuclei through which are supplied the muscles of visceral origin through cranial

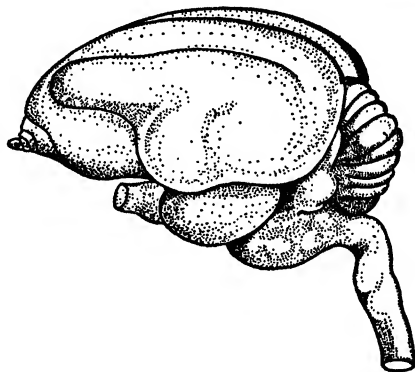


FIG. 144C. Lateral view of parrot brain. Note the smooth surface, the relatively large cerebral hemispheres and cerebellum in comparison with the alligator brain.

nerves V, VII, IX, X, and XI. These nuclei are the ambiguous, the motor nucleus of the fifth and seventh, and the dorsal nucleus of the vagus nerve. The latter supplies smooth muscles and glandular tissue through special visceral motor fibers.

The somatic motor column on the floor of the medulla includes the nuclei which supply, through cranial nerves III, IV, VI, and XII, the striated muscles of myotomic origin, *i.e.*, the extrinsic muscles of the eye and tongue.

The nervus terminalis, the first cranial nerve (sensory), is found in all vertebrates, but since it was discovered after the others had been numbered and named, no numerical designation is given to it. Its fibers, in close communication with the olfactory tract, pass to the nasal mucosal region.

I. *The Olfactory Nerve (Sensory)* (Fig. 153). The olfactory nerve is distributed by a number of filaments to the olfactory membrane. It has a variable number of fibers, some 20 in man and a larger number in the fishes. These fibers join in the olfactory bulb, which is continuous with the olfactory tract and the olfactory lobe. The only nerve that originates in the telencephalon, it represents an outgrowth of the brain, as does the optic, in contrast to the remaining 10 cranial nerves, which are probably originally derived from spinal nerves.

II. *Optic Nerve (Sensory)* (Fig. 143). The optic nerve, associated with the retina and the floor of the diencephalon, embryonically is an outgrowth of the brain. Its embryonic development will be considered in connection with the description of the eye. In passing to the diencephalon, the medial fibers of either side cross to the other and thus create the optic chiasma on the brain floor just anterior to the hypophysis. The optic tract extends from the diencephalon to the mesencephalon. In many fishes the crossing of the fibers is complete; in the mammals it is incomplete.

III. *Oculomotor Nerve (Mixed)* (Fig. 143). The oculomotor nerve is associated with the mesencephalon. It is a motor nerve to the following four extrinsic eye muscles, rectus superior, inferior, medialis, and obliquus inferior, and to the levator palpebrae superioris, which lifts the upper eyelid. Oculomotor, trochlear, and abducens nerves associate with the myotomes destined to form the extrinsic eye muscles. They are somatic motor nerves, although with the oculomotor we find visceromotor and viscerosensory fibers which associate with the ciliary ganglion. In man there are 12 to 15 short ciliary nerves to the ciliary muscle of the eyeball and to the iris and cornea. Some of the ciliary ganglion fibers are sensory, contributed by the nasociliary branch of the trigeminal nerve; others are sympathetic, to the blood vessels of the eyeball.

IV. *Trochlear Nerve (Motor)* (Fig. 146). This is a somatic motor nerve associated with the mesencephalon and directed to the superior oblique eye muscle. It enters the optic orbit above the eye muscles and pierces the orbital surface of the muscle. Proprioceptive afferent fibers occur in the nerve; hence strictly speaking it is a mixed nerve.

V. *Trigeminal Nerve (Mixed)* (Fig. 146). This is sensory to the superficial and deep portions of the head and face and motor to the muscles of mastication. Its motor roots arise in the medulla and pons; its sensory root, much larger than the motor, emerges from the semilunar ganglion (gasserian) outside the brain. The ganglion sends fibers to the main sensory nucleus in the pons and to the nucleus of the spinal tract of the trigeminal nerve in the medulla oblongata.

Three large sensory trunks emerge from the semilunar ganglion. They are the *ophthalmic*, *maxillary*, and *mandibular* nerves. In fishes the ophthalmic trunk is divided into a superficial and a deep branch traversing the posterior region of the orbit and passing to the rostrum. These branches are sensory to the snout region. In mammals only the homologue of the deep ophthalmic nerve is retained. It divides into frontal, nasociliary, and lacrimal branches to the forehead, nose, and region about the eyes and some of the head sinuses.

The maxillary nerve, sensory to the sides of the head in the classes below the mammals, in man is distributed to the meninges, the cheeks, the upper lips, and the face, and it sends alveolar branches to the teeth of the upper jaws. It also has a sensory distribution to the tonsils, soft palate, and nasal pharynx.

The mandibular nerve has a sensory distribution to the skin of the temples, lower jaw, chin, teeth of the lower jaw, and gums and a motor deployment to the masseter, temporal, and pterygoid muscles in mammals and to the homologues of these muscles in lower forms. Through its lingual branch, which is sensory, the taste buds of the anterior two-thirds of the tongue are innervated.

Motor fibers of the mandibular nerve supply the masseter, temporal, and pterygoid muscles. Four sympathetic ganglia are associated with the trigeminal nerve. On the medial surface of the mandibular nerve a small reddish *otic ganglion* communicates with the internal pterygoid branch of the mandibular nerve, as well as with the facial and glossopharyngeal nerves. It sends filaments to the tensor tympani muscle and the tensor veli palatini.

Near the posterior wall of the orbit, lateral to the optic nerve, the small *ciliary ganglion* is related to the trigeminal nerve through the long ciliary branch of the ophthalmic, to the oculomotor nerve by a short ciliary root, and to the sympathetic nervous system by a slender filament. It sends out short branches to the cornea, iris, and ciliary muscle of the eye.

The *sphenopalatine ganglion*, associated with the maxillary branch of the trigeminal nerve through the greater superficial petrosal nerve, has orbital branches to the lacrimal gland, palatine to the pharynx, and nasal to the mucous membrane of the nose.

The *submaxillary ganglion* is associated with filaments of the lingual branch of the trigeminal nerve, with the facial nerve through its chorda tympani branch, and with the sympathetic nervous system through the superior cervical ganglion. It supplies the mucous membrane of the mouth, the duct of the submaxillary gland, and the sublingual glands.

VI. *The Abducent Nerve (Motor)* (Fig. 146). The sixth cranial nerve is a motor nerve to the lateral (external) rectus muscle of the eye. Its fibers arise in the region of the rhomboid fossa of the medulla oblongata and emerge at the lower border of the pons. It becomes associated with the medial side of the muscle immediately upon its emergence into the orbit. Proprioceptive afferent fibers from the lateral rectus muscle are associated with it.

VII. *The Facial Nerve (Mixed)* (Fig. 146). Like the trigeminal, glossopharyngeal, and vagus, the facial was originally a branchial nerve. In its distribution it reveals its visceral origin, since it supplies muscles originally derived from and associated with the branchial arches. In fishes it is the nerve of the spiracle and the hyoid arch, in addition to its distribution to the snout and its association with the lateral line system. It has, in common with the spinal nerves, a dorsal and a ventral ramus. The dorsal ramus, entirely sensory, divides into cutaneous and lateral branches, the latter supplying the lateral line region of the snout and the mandible. Both cutaneous and lateral line branches are lost in land vertebrates. Originally the dorsal ramus gave rise to a pretrematic, a pharyngeal, and a posttrematic branch. The first supplied viscerosensory fibers to the anterior wall of the visceral pouch, the pharyngeal contributed sensory fibers to the lining of the pharynx, while the posttrematic was sensory to the posterior wall of the visceral pouch and motor to the adjacent branchial muscles.

This pattern is somewhat obscure in the fishes and becomes greatly modified in land forms with the loss of gills and the lateral line system. In the dogfish, a superficial ophthalmic, a buccal, and hyomandibular branches represent the dorsal ramus indicated above. They supply the supraorbital and infraorbital, mandibular, and hyomandibular portions of the lateral line system. In addition, the hyomandibular branch carries motor fibers to the hyoidean muscles. A palatine nerve emerges from the geniculate ganglion, in common with the hyomandibular trunk, to supply sensory fibers to the roof of the mouth.

In mammals the seventh continues as a mixed nerve. Its *special visceral motor* fibers are distributed to the muscles of facial expression, the scalp, platysma, stapedius, posterior belly of the digastric, and stylohyoid muscles. Its *general visceral motor fibers* pass to the submaxillary ganglion by way of the chorda tympani, from which they are distributed to the lacrimal, submaxillary, and sublingual glands. These fibers convey vasomotor and secretory impulses. Its *sensory portion*, also called the *nervus intermedius*, takes origin at the geniculate ganglion and provides deep sensation to the face. A group of *special visceral*

afferent fibers, the *chorda tympani* and *lingual nerves*, innervate the taste buds of the anterior two-thirds of the tongue. Some sensory fibers from the geniculate ganglion pass by the greater superficial petrosal nerve to the sphenopalatine ganglion and thence to the mucous membrane of the soft palate, mouth, upper pharynx, and nose.

In amniotes the original character of the facial as a branchial nerve to the hyoid arch is lost. Its motor branches are distributed to the posterior belly of the digastric, stylohyoid, platysma, and facial muscles, all of branchial origin. The palatine branch in the fishes probably corresponds to the greater superficial petrosal nerve of the mammals, while the mandibular branch in the fish appears homologous to the *chorda tympani* of mammals.

VIII. *The Acoustic Nerve (Sensory)* (Fig. 140). The eighth cranial nerve is purely sensory. In fishes it is concerned with balance through its distribution to the semicircular canals, the sacculus, and the utricle. In mammals, birds, reptiles, and amphibians, where hearing is added to the function of equilibration, it divides into a vestibular nerve of balance and a cochlear nerve of hearing. The latter originates in the spiral ganglion of the cochlea with peripheral branches ending in the organ of Corti (see description of the ear, page 304). It is classified as a special somatic afferent nerve. The vestibular nerve originates in the vestibular ganglion, which lies in the internal auditory meatus; its central branches end in the vestibular nuclei of the pons and medulla, with some passing directly to the cerebellum. Its peripheral distribution is, as indicated, to the semicircular canals, the sacculus, and the utricle.

IX. *The Glossopharyngeal Nerve (Mixed)* (Fig. 146). This is one of the branchial nerves originally associated with the gills and the lateral line system. Its sensory components originate in the petrosal ganglion. In the fishes it supplies the second gill pouch and retains its primitive character more nearly than do any of the remaining cranial nerves. From the petrosal ganglion, which is epibranchial in the fishes, emerge pretrematic, pharyngeal, and posttrematic divisions. The pretrematic carry sensory fibers to the anterior gill wall; the posttrematic provide visceral sensory fibers to the posterior gill wall, and visceral motor fibers pass to the branchial muscles associated with the third branchial arch. The pharyngeal division contributes viscerosensory fibers to the lining of the pharyngeal cavity.

In mammals the nerve emerges through the jugular foramen of the skull in its own sheath; vagus and accessory nerves emerge through the same opening. At its point of emergence is the *superior ganglion*, a

probable offshoot of the *petrosal ganglion* and medial to it. *Visceral afferent fibers* are distributed to the taste buds of the posterior third of the tongue and to the pharynx. *Visceral efferent fibers* join the otic ganglion, from which secretory fibers deploy to the parotid gland; others pass directly to the stylopharyngeal muscle. As its name indicates, the nerve passes largely to the tongue and pharynx. The glossopharyngeal nerve also has carotid branches, which terminate in special end organs in the carotid sinus and convey pressure impulses to the medulla. It is active in the regulation of blood pressure.

X. *The Vagus Nerve (Mixed)* (Fig. 146). The term *vagus* means wanderer; the name applies because of the wide distribution of the nerve. It probably represents a fusion of several nerves, since its visceral trunk supplies the four posterior gills in the fishes, each branch with its own pre- and posttrematic and pharyngeal divisions, each with its own epibranchial ganglion except in some of the bony fishes, where a partial fusion of the ganglia is correlated with the reduction of the gill apparatus. The *visceral trunk* continues to the heart and the digestive tract. The *lateral vagus trunk* in the fishes is sensory from the lateral line system.

In amniotes, with loss of the lateral line and gills, only a small somatic sensory component remains. This passes from the jugular ganglion to the external auditory meatus and the back of the ear. A more prominent *visceral sensory component* arises from the *nodosal ganglion* (this ganglion probably represents the fused epibranchial ganglia of the fish). It conveys sensory fibers to the pharynx, larynx, trachea, and viscera. *Visceral motor fibers*, forming the internal laryngeal nerve, also pass from the nodosal ganglion to the intrinsic muscles of the larynx.

The motor fibers to the thoracic and abdominal viscera descend to parasympathetic ganglia in the vagal plexuses of the viscera and continue to the end organs as postganglionic fibers. Special cardiac and pulmonary plexuses innervate the heart and the lungs.

To sum up: The nerve carries somatic sensory fibers to the skin of the ear and the external auditory meatus; general visceral sensory fibers to the thorax and digestive tract; special visceral sensory fibers to the intrinsic muscles of the larynx; and visceral motor fibers to the thoracic organs and digestive tract and to the muscles of the pharynx and larynx.

XI. *The Accessory Nerve (Motor)* (Fig. 146). This nerve has both a cranial and a spinal root. It first appears as a branch of the vagus root in amniotes. It supplies the trapezius and the sternocleidomastoid muscles, the latter derived from the trapezius. Some of its fibers are associated with the visceral fibers of the vagus in the thoracic and abdominal viscera; others pass with the vagal fibers to the striated muscles of the larynx and pharynx.

XII. *The Hypoglossal Nerve (Motor)* (Fig. 146). Both eleventh and twelfth cranial nerves first appear as distinct cranial additions in the amniotes. The twelfth is a somatic motor nerve to the tongue and infrahyoid muscles. These muscles are of hypobranchial origin, and their innervation may arise from the medulla by several ventral roots. In amphibians, the tongue is supplied by one to three pairs of spinal nerves that may be homologous to the hypoglossal nerve of higher vertebrates. In elasmobranch fishes a spinooccipital nerve foreshadows the hypoglossal. In bony fishes, however, there is a direct transition from the tenth cranial nerve to spinal nerves.

Spinal Nerves. Phylogenetically spinal nerves probably precede the cranial. Protochordates like *Amphioxus* without a well-defined brain or head have both dorsal (sensory) and ventral (motor) nerves associated with the spinal cord, as well as nerves of this same character emerging from the primitive brain. In *Amphioxus* sensory and motor nerves do not unite in a common mixed nerve but remain separate throughout their course. Thus we speak not of dorsal and ventral nerve roots but of dorsal and ventral nerves in these cephalochords.

Amphioxus and the cyclostomes exhibit another peculiarity in connection with the emergence of the spinal nerves from the cord in that the dorsal and ventral nerves alternate. The dorsal, or sensory, emerge from the cord and pass peripherally in the myosepta, with ventral visceral branches to the internal organs. The original peripheral destination of these afferent nerves was the integument, and they traverse the divisions between the myomeres to reach it. The ventral, or motor, nerves pass from the cord directly into the adjacent myomeres. This alternation persists in some of the teleost fishes. In the remaining craniotes, dorsal and ventral nerve roots emerge one above the other, each pair at the same level in the cord.

The peripheral end of the dorsal nerve beyond its cell body represents its dendritic extension. The cell bodies of many nerve fibers form the spinal ganglion. Each sensory nerve has its own spinal ganglion from whose medial portion the axons of the individual fibers pass into the cord as the dorsal root of the nerve. The origin of these spinal ganglia from the neural crests during embryonic development has been discussed elsewhere (page 210). It will be recalled that in some of the cyclostomes and teleost fishes the spinal ganglia may be incorporated in the dorsal horns of the spinal cord. In all the remaining adult vertebrates they are exterior to the cord. The neurites (axons) passing into the cord from these ganglia connect secondarily with association cells, which in turn form synapses with dendrites of nearby motor cells and thus establish the structural basis for reflex actions; or they ascend in tracts to

higher levels of the cord and the brain. They are not limited to ascending the cord, however, since, by forking, one arm of the dendrite may descend to make secondary synapses with association cells at lower cord levels. The spinal cord may be looked upon in part as a continuation

of the nerves banding together in tracts to reach higher levels of the cord and brain and in part as reflex centers to which sensory nerves are directed from the periphery and from which motor nerves extend to the muscular and glandular systems. Their detailed relations to the spinal cord and brain have been discussed in the description of the central nervous system (page 213).

The motor, or ventral, spinal nerves, in contrast to the peripheral ends of the sensory, represent the axons of nerve fibers whose cell bodies remain within the substance of the spinal cord, specifically in its ventral and ventrolateral horns. Shortly after emergence from the cord the ventral root, in chordate levels above *Amphioxus* and the myxinoids, joins the dorsal beyond the spinal ganglion, to form a mixed nerve. This mixed nerve divides further into a dorsal (posterior) ramus which supplies the back of the animal and a ventral (anterior) ramus to its ventral and lateral aspects. It must be remembered that both rami carry sensory as well as motor fibers. In the course of their distribution, the sensory and motor elements of these nerves separate; the former pass largely to the skin and the articulations, although some extend to visceral organs, while the motor fibers supply the muscles.

Associated with the dorsal and ventral spinal nerve roots are visceral sensory and visceral motor fibers; the latter constituting the peripheral elements of the sympathetic nervous system, as already described.

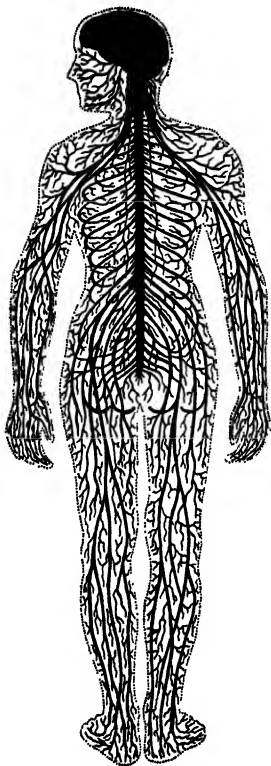


FIG. 145. Distribution of spinal nerves in the human body. The spinal cord ends at the level of the second lumbar vertebra. Lumbar and sacral nerves descend almost vertically to their points of exit from the cord. The spinal nerves extend symmetrically to the two sides of the body.

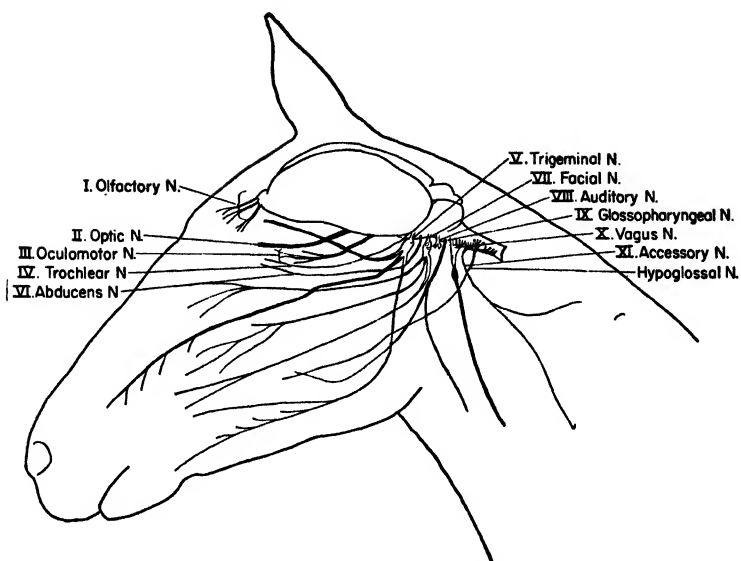


FIG. 146 Cranial nerves of the horse (diagrammatic).

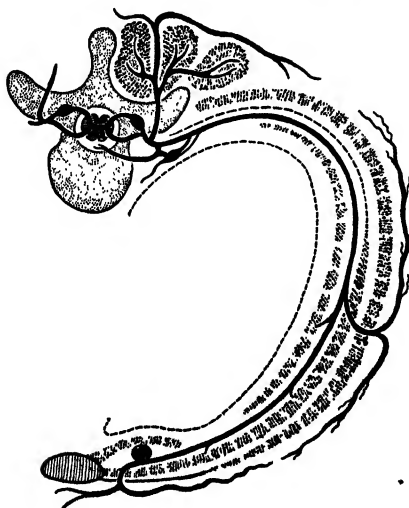


FIG. 147. Cross-sectional view of a typical spinal nerve, its distribution and relation to the spinal cord. (After Gray.)

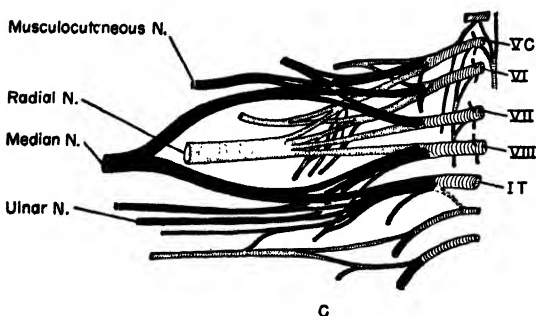
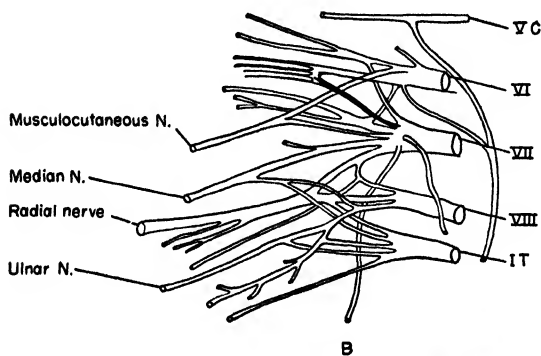
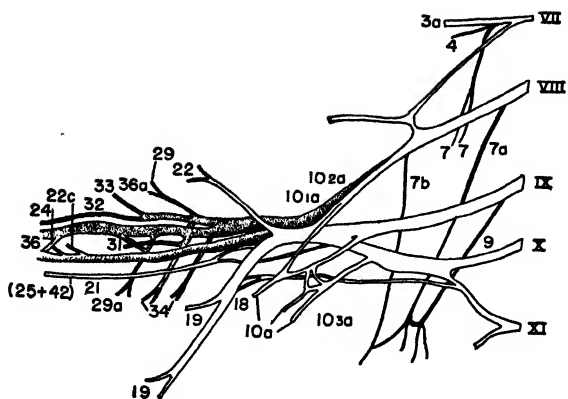


FIG. 148. A, brachial plexus, alligator. Roman numerals indicate the spinal nerves involved. This nerve distribution supplies the shoulder, pectoral muscles, upper arm, forearm, and hand. B, brachial plexus, cat. C, brachial plexus, man. (Redrawn from Bronn.)

The distribution of both the sensory and the motor nerve fibers is highly precise and stems from the original metameric arrangement of the body musculature and its associated innervation. Figures 145 and 147 show the dorsal and ventral cutaneous distribution in the human body, the segmental nature of the innervation, as well as the original myomeric arrangement of the back muscles. The segmental nature of the motor distribution is more obscured because of the great transformation of the various muscle segments, but dissection still reveals the basic metameric pattern, particularly in the back and intercostal muscles.

In the neck, lumbar, and sacral regions of the mammal, and to a certain extent in the lower vertebrates, the spinal nerves have united to form elaborate plexuses (Fig. 148). The first indication of such plexus formation appears in the innervation of the fish fin. In addition to the nerves running segmentally and quite independently of each other to the muscle slips of the fins, a collector nerve has evolved. This is the first nerve in the series directed to the appendages, and its fibers, instead of passing independently, cross and join the nerves lying posteriorly in the sequence. In reptile, bird, and mammal, this plexus formation includes the spinal nerves of the neck, where a distinct cervical and a brachial plexus take their origin, and a lumbosacral plexus, which represents a confluence of the nerves passing to the pelvic appendage.

The entire shoulder, arm, forearm, and hand innervation of man or of any typical mammal, for that matter, originates with some minor exceptions from this brachial plexus. The lumbosacral plexus, a serial homologue of the brachial, illustrated in Fig. 149, indicates the innervation to the pelvic and the posterior limb musculature and integument. Both motor and sensory nerves are represented in the plexuses. Plexus

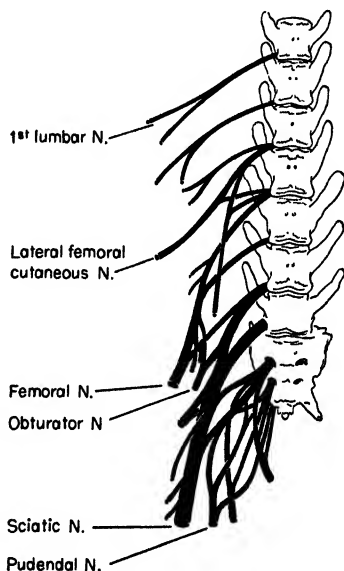


FIG. 149. Lumbosacral plexus of the dog. This nerve distribution supplies the lower portions of the trunk, but tocks, external genitalia, tail, and the hindlimbs. The plexus includes nerves from the first lumbar to the last sacral inclusive.

formation is associated with the many adaptive modifications that have taken place in the musculature; the nervous system, because of its conservative nature, insists upon sending its nerves to the muscle segment it has supplied at fish or earlier levels, regardless of subsequent transformations in the segment. If, for example, a muscle segment differentiates into several small muscles that in time may be no longer associated with each other, the original nerve through its branching will still innervate the several slips.

Table 7 indicates the chief sensory and motor nerves emanating from these plexuses as well as their general destinations; while based upon the human pattern, the distribution holds quite generally for the remaining mammals.

TABLE 7. BRACHIAL PLEXUS: SENSORY AND MOTOR DISTRIBUTION

<i>Nerve</i>	<i>Region innervated</i>
Sensory distribution	
Musculocutaneous 5,6,7C.....	Dorsal and lateral region of forearm
Medial brachial cutaneous 8C, 1T....	Medial aspects of upper arm and forearm
Medial antibrachial cutaneous 8C, 1T	
Palmar branches of median 6,7,8C, 1T	Skin of thumb, palm, and digits including lateral half of 4th digit
Palmar branches of ulnar 8C, 1T.. .	Palm and dorsum of hand including medial half of 4th and all of 5th digit
Cutaneous branches of radial 5,6,7,8C, 1T.....	Part of dorsum of forearm and hand on thumb side
Cutaneous branches of axillary 5,6C.	Skin over lower part of deltoid muscle
Motor distribution	
Phrenic 4,5C.....	Diaphragm
Dorsal scapular 5C.....	Rhomboid muscles
Suprascapular 5,6C.....	Supra- and infraspinatus muscles
Subclavius 5,6C.....	Subclavius
Lateral and medial anterior thoracic 5,6,7,8C, 1T.....	Pectoralis muscles
Musculocutaneous 5,6,7C.....	Biceps brachii, coracobrachialis, brachialis
Median 6,7,8C, 1T.....	Most of the flexors of forearm, wrist, and hand
Ulnar 8C, 1T.....	Deep flexors and part of superficial flexors of the fingers
Radial 5,6,7,8C, 1T.....	Extensors of upper arm, wrist and hand
Axillary 5,6C.....	Abductors of arm and the teres minor
Upper and lower subscapularis 5,6C..	Subscapular and teres major muscles
Long thoracic 5,6,7C.....	Serratus anterior
Thoracodorsal 5,6,7C.....	Latissimus dorsi

The trapezius and sternocleidomastoid muscles, the latter a derivative of the trapezius, are supplied by the eleventh cranial nerve, the

spinal accessory. The regions over the ventral and dorsal parts of the shoulder receive their sensory distribution from the supraclavicular nerves which originate from the third and fourth cervical nerves by way of the cervical plexus.

In the human body the twelfth thoracic, all five lumbar, and four sacral nerves enter into the formation of the lumbosacral plexus (Table 8). In addition the fifth sacral and the coccygeal nerves form a small coccygeal plexus.

TABLE 8. LUMBOSACRAL PLEXUS: SENSORY AND MOTOR DISTRIBUTION

<i>Nerves</i>	<i>Region supplied</i>
Sensory distribution	
Lateral and anterior cutaneous branches of iliohypogastric, 1L....	Skin of gluteal and of hypogastric region
Ilioinguinal 1L.....	Skin of upper and medial part of thigh, of the root of penis, upper part of scrotum, mons pubis, labium majus
Genitofemoral 1L, 2L.....	Skin of scrotum
Lumboinguinal branch of genitofemoral	Skin of anterior and upper part of thigh
Lateral femoral cutaneous 2, 3L (anterior and posterior branches).....	Anterior, lateral, and posterior aspects of thigh to the knee
Obturator 2, 3, 4L.....	Skin on tibial side of leg; articular branch to hip joint; articular branches to knee
Femoral 2, 3, 4L.....	Skin on anterior aspect of thigh to knee; medial side of thigh and leg, infrapatellar region, front and medial side of leg; articular branches to hip joint
Posterior femoral cutaneous 5L, 1, 2, 3S	Skin of perineum, posterior surface of thigh and leg
Sciatic, sural, lateral dorsal cutaneous, medial plantar, lateral plantar 4, 5L, 1, 2, 3, 5.....	Skin of foot and toes, sole of foot, digits and their articulations
Common peroneal, cutaneous branches 4, 5L, 1, 2S.....	Posterior and lateral surface of leg
Superficial peroneal branch of common peroneal.....	Skin on dorsum of ankle and foot
Pudendal plexus 2, 3, 4S.....	Scrotal and labial (majus) sensory distribution
Coccygeal plexus 5S, 1, coccygeal....	Skin in region of coccyx
Iliohypogastric 1L.....	Twigs to abdominal muscles
Iliolinguinal 1L.....	Twigs to abdominal muscles
Genitofemoral 1, 2L.....	Cremaster muscle
Obturator 2, 3, 4L (anterior and posterior branches).....	Adductor and obturator externus muscles

TABLE 8. LUMBOSACRAL PLEXUS: SENSORY AND MOTOR DISTRIBUTION
(Continued)

<i>Nerves</i>	<i>Motor distribution</i>	<i>Region supplied</i>
Femoral 2,3,4L (saphenous branch)	Quadriceps femoris	
Sacral plexus, small (direct branches)	Quadriceps femoris, gemelli, piriformis, superior and inferior gluteal muscles	
Sciatic branches 4,5L, 1,2,3S.....	Hamstring muscles	
Tibial branch of sciatic.....	Gastrocnemius, plantaris, soleus popliteus	
Medial plantar branch of tibial, lateral plantar branch of tibial.....	Abductors and flexors of toes, interossei, lumbricales	
Common peroneal branch of sciatic..	Extensors and everters of foot and toes	
Pudendal plexus 2,3,4S.....	Levators and sphincters ani, coccygeus, perineal, cavernosus, urethral sphincter muscles	
Coccygeal plexus 5S.....	No muscular branches	

THE AUTONOMIC NERVOUS SYSTEM

The term *autonomic nervous system* designates the two functional subdivisions of the visceral nervous system (Fig. 150). One of these is the sympathetic, or *thoracolumbar outflow*, since its emergence is restricted to the thoracic and lumbar regions; the other is the parasympathetic, or *craniosacral outflow*, whose emergence is restricted to the brain and the sacral portion of the cord. It should be emphasized that this is a functional designation, since structurally elements of the craniosacral outflow are part of the cranial and sacral nerves. It controls a wide variety of actions, including the heart rate, blood pressure in part, secretory activities of glands, tonicity of the smooth muscle walls of the intestine, bronchi and blood vessels, activities of the reproductive organs, and sweat secretion. This dual system thus is directed to the smooth muscles, including those of the circulatory and the digestive systems, the glands of external secretion, and the heart. It influences secretion of the endocrine glands as well. The system is outside voluntary control, hence its name. In other words, the many activities of the body of which we are commonly unaware and which we take for granted are faithfully carried out by this truly autonomous system.

It has its own ganglia that make it partially independent of the central nervous system. It is associated with the central system, however, through the white sympathetic communicating rami and the parasympathetic roots, to be described. The craniosacral outflow is associated with cranial nerves III, VII, IX, and X and with sacral nerves 2 and 3; the thoracolumbar, with thoracic nerves 1 to 12 and lumbar 1 and 2.

The significance of these relationships will be better understood after consulting Fig. 150.

The Sympathetic Nervous System. It will be recalled that the dorsolateral column of cells, identified in the spinal cord, represents nuclei of the sympathetic nervous system. The axons of the cells of the lateral gray horn were described as passing out with the ventral motor roots of the spinal nerves to form preganglionic fibers or white communicating rami. These myelinated fibers terminate in the higher vertebrates in segmentally arranged chain ganglia. In the ganglia

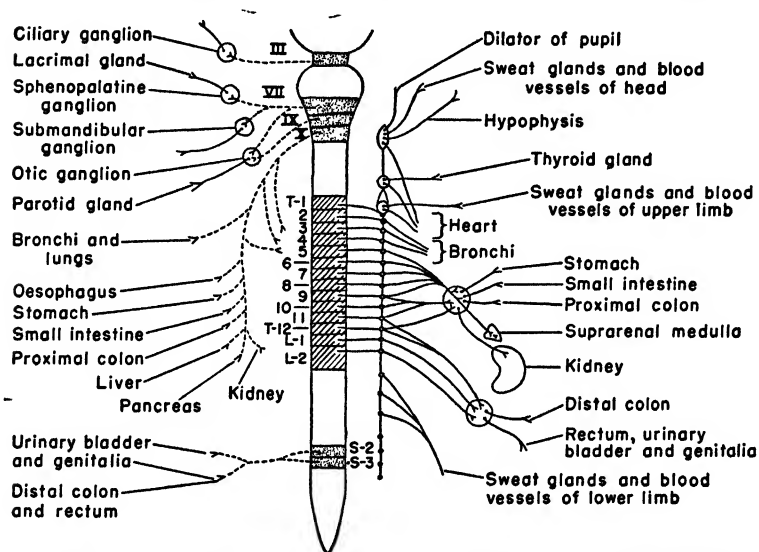


FIG. 150. The autonomic nervous system. (Redrawn from Cunningham.)

these axons synapse with dendrites of cells whose axons pass as postganglionic fibers to the smooth muscles and glands. Not all the preganglionic fibers terminate in the ganglia at the level of their emergence. Some pass to higher or lower levels in the sympathetic trunk; others pass directly to the prevertebral plexuses before terminating. A single preganglionic axon may give off a number of collaterals which synapse with a number of postganglionic fibers.

The ganglia of the sympathetic system are of three types:

1. Central, or paravertebral, ganglia, also called chain ganglia, usually segmentally arranged in the sympathetic trunk. In man, 3 pairs are found in the cervical, 10 or 11 pairs in the thoracic, 4 pairs each in

the lumbar and sacral regions. From these ganglia postganglionic fibers are distributed.

2. Collateral, or prevertebral, ganglia associated with thoracic, abdominal, and pelvic plexuses. From the plexuses nerve fibers are distributed to physiologically related organs.

3. Terminal ganglia (myenteric and submucosal) in the intestinal walls supplied largely by parasympathetic fibers.

The sympathetic nervous system is associated also with the spinal nerves through gray communicating rami. These are groups of non-medullated fibers extending from the chain ganglia to the spinal nerves. These postganglionic fibers, through this association, become the vasomotor (to vessel walls), sudomotor (to sweat glands), and pilomotor (to muscles raising the hair) components of the spinal nerves. In addition, the gray rami may contain some medullated afferent fibers which pass via the dorsal nerve roots and thence into the spinal cord.

Although the thoracolumbar outflow of the sympathetic system has its central connections limited to the thoracic and lumbar regions of the spinal cord, sympathetic distribution extends into the head, cervical, and pelvic regions. This is brought about by an extension of the ganglionated sympathetic trunk into the neck and the pelvis. In the neck three ganglia, a superior, middle, and inferior, are interconnected by fibers of the sympathetic trunk. White communicating rami of the upper thoracic region of the cord enter the sympathetic trunk and ascend in the cervical sympathetic trunk to the levels of the three indicated ganglia. From the *superior cervical ganglion*, fibers are distributed by the gray rami to the upper four cervical nerves and filaments to the vagus and hypoglossal nerves. A plexus from the superior ganglion ascends with the external and internal carotid artery, surrounding the latter to its termination in the brain case. Other branches pass to the pharynx, the heart (superior cardiac nerve), the petrous ganglion of the glossopharyngeal nerve, the jugular ganglion of the vagus, and the geniculate ganglion of the facial nerve.

The *middle cervical ganglion* gives rise to gray communicating rami which pass peripherally with the fifth and sixth cervical nerves. It sends a middle cardiac branch to the heart and usually small twigs to the thyroid gland along the inferior thyroid artery. It communicates with the inferior cervical ganglion by the ansa subclavia, a nerve loop around the subclavian artery.

The *inferior cervical ganglion* is commonly fused with the first thoracic ganglion, when it is called, because of its shape, the stellate ganglion. It lies partly within the thorax at the level of the head of the first rib. Gray rami communicantes from the ganglion accompany

the seventh and eighth cervical nerves in man; it sends an inferior cardiac nerve to the heart and plexuses to the subclavian artery and its tributaries.

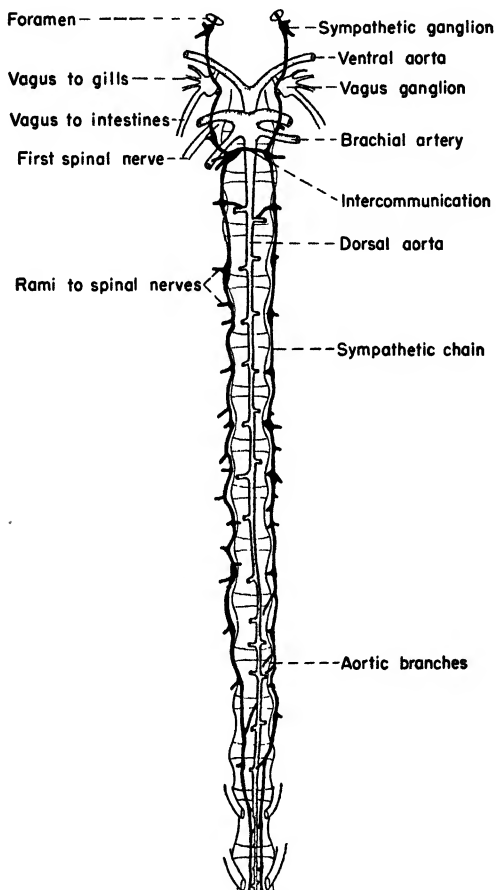


FIG. 151A. Sympathetic nervous system of the barracuda.

The thoracic distribution of the sympathetic nervous system is by way of the segmental chain ganglia (Fig. 151 A, B). Fibers from the upper ganglia supply the cardiac, aortic, and pulmonary plexuses. Gray rami from these ganglia pass to the thoracic spinal nerves. The fibers from the lower thoracic ganglia, beginning with the fifth or sixth ganglion

in man, combine to form greater, lesser, and least splanchnic nerves. The greater splanchnic nerve descends along the thoracic wall, pierces the diaphragm, and passes to the celiac ganglion in the abdomen; the lesser and least pass to the renal ganglion and plexus.

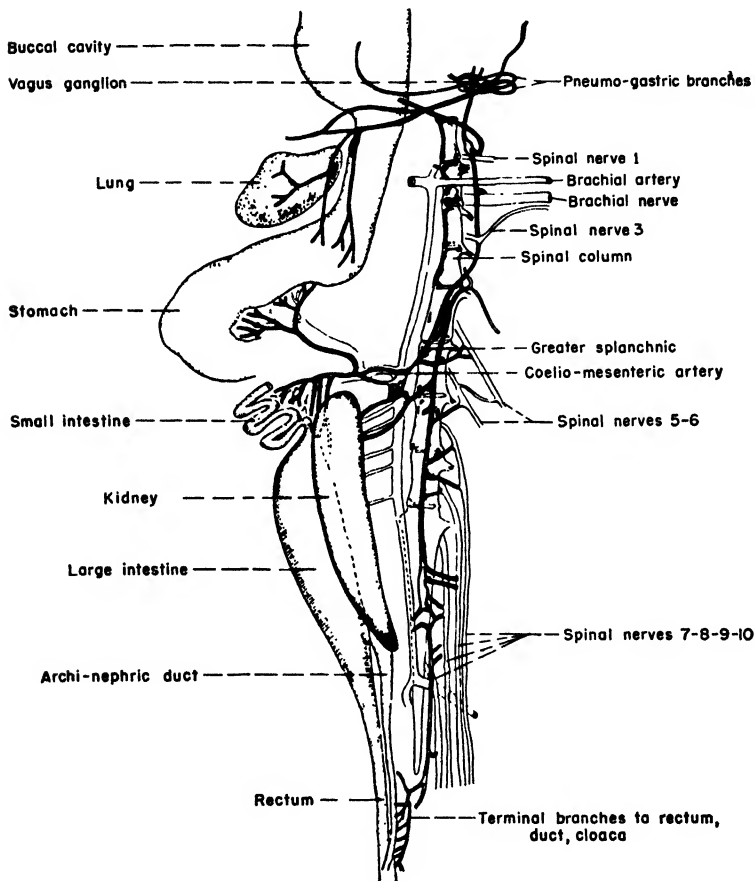


FIG. 151B. Sympathetic nervous system of the frog.

In the abdominal region the sympathetic chain ganglia diminish in size, and the entire chain extends more medially over the bodies of the vertebrae. In man four pairs of abdominal ganglia occur. Their gray rami pass out with the lumbar spinal nerves to be distributed to the

vessels, the sweat glands, and erector pilae muscles of the region. Branches from the ganglia are also distributed to the abdominal, aortic, and hypogastric plexuses. The chief plexuses in the abdomen are the celiac (the largest), phrenic, superior and inferior mesenteric, aortic, and hypogastric. Hepatic, suprarenal, and lineal plexuses accompany the arteries to the liver, adrenal, pancreas, and spleen (Fig. 152).

In the pelvis the sympathetic trunk contains four to five small ganglia on each side, and the two trunks join at the level of the coccyx in a

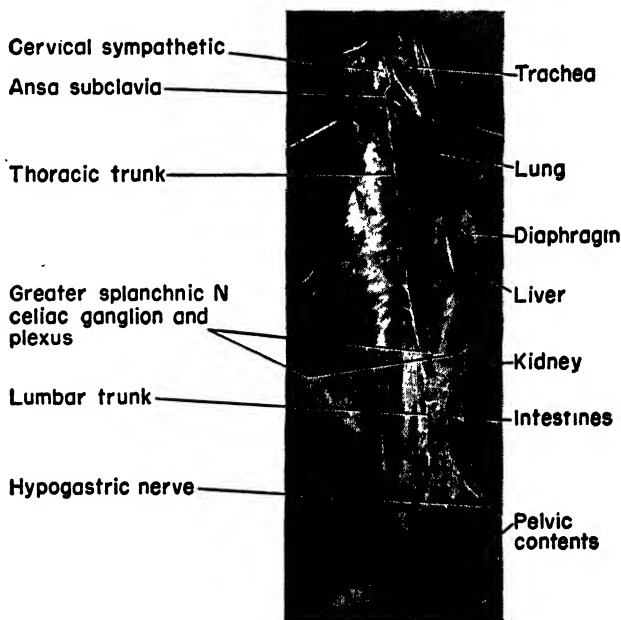


FIG. 152. Sympathetic nervous system of the monkey (*Cebus capucinus*).

small coccygeal ganglion, the ganglion impar. Since sympathetic representation does not extend in the spinal cord below the level of the second or third lumbar vertebra, the white rami from the lower thoracic and lumbar region pass downward into the pelvic portion of the sympathetic trunk. Gray rami pass outward with the sacral and coccygeal nerves. The pelvic plexuses are formed by contributions from these lumbar ganglia. Chief of these plexuses are the hemorrhoidal, vesicular, prostatic, cavernosus, vaginal, and uterine, associated with rectum, bladder, prostate, penis, vagina, and uterus.

The Parasympathetic Nervous System, or Cranial-Sacral Outflow.

The cranial outflow is largely efferent (visceral motor) in nature, with some afferent fibers associated with the oculomotor, facial, glossopharyngeal, and vagus nerves (Fig. 150). The nuclei for these visceral motor elements arise in the brain stem. The parasympathetic fibers associated with the oculomotor nerve originate from cells in the Edinger (Westphal) nucleus; those with the facial from the superior salivatory nucleus; those with the vagus from the dorsal nucleus of the vagus. Visceral afferent taste fibers are associated with the facial and the glossopharyngeal, vasosensory fibers from the carotid sinus and carotid body with the glossopharyngeal, afferent fibers from the digestive tract and lungs with the vagus nerve.

The preganglionic fibers associated with the oculomotor nerve terminate in the ciliary ganglion. From the ganglion short postganglionic ciliary motor nerves extend to the ciliary muscles and the iris. The preganglionic fibers with the facial nerve are the greater superficial petrosal and the chorda tympani nerves; the first passes to the sphenopalatine ganglion, where postganglionic fibers synapse with it, and these secretory fibers supply the mucous membrane of the nasal cavity, the palate, and the lacrimal glands. The preganglionic fibers represented by the chorda tympani pass to the lingual branch of the trigeminal nerve and thence to the submaxillary ganglion. From the ganglion, postganglionic secretory and vasodilator fibers extend to the submaxillary, sublingual, and intrinsic glands of the tongue.

The preganglionic visceral motor fibers of the glossopharyngeal nerve descend as the lesser superficial petrosal nerve to the otic ganglion, where postganglionic secretory and dilator fibers continue to the parotid gland and mucous membrane of the mouth and tongue.

The preganglionic visceral motor fibers of the vagus nerve terminate in small ganglia in the organs they supply. These ganglia lie in the heart wall, bronchi, and myenteric and submucosal plexuses within the intestinal wall. From these ganglia and plexuses, postganglionic fibers carry the innervation to the end organs.

The sacral parasympathetic nerves originate in the sacral part of the spinal cord and emerge with the anterior primary rami of the second, third, and fourth sacral nerves. After reaching the pelvic plexuses they apparently synapse with the postganglionic fibers to the large intestine, rectum, anus, bladder, and genitalia.

Functions of the Autonomic System. The internal organs are innervated by both sympathetic and parasympathetic branches of the autonomic nervous system. The actions of the two divisions generally

are antagonistic, although this is not invariably so. The heartbeat, for example, is depressed by vagal and accelerated by sympathetic stimulation. Intestinal motility is inhibited by sympathetic innervation and increased by vagal. The sympathetic system acts as a vasoconstrictor, although the peripheral vessels receive sympathetic dilators as well. The pupil is constricted by the parasympathetic component of the oculomotor nerve and dilated by impulses mediated through the sympathetic fibers from the superior cervical ganglion. The autonomic system controls temperature, heart action, bladder contraction, peristalsis, and behavior of the genital organs in emotional states and in copulation, to mention some of the common functions. The centers through which the system exerts its influence have been touched on briefly. To summarize them: The cranial outflow of the parasympathetic system is regulated through nuclei associated with the oculomotor, facial, glossopharyngeal, and vagus nerves. The cells of origin for the sacral outflow lie in the sacral portion of the spinal cord. A vasoconstrictor center has been located in the medulla, to which afferent impulses from the glossopharyngeal and vagus nerves are transmitted. In the floor of the fourth ventricle is a center for the regulation of sugar metabolism; a respiratory center is near the inferior olive. Other centers are in the hypothalamus; reactions of fear and rage may be elicited through stimulation of this region. Cortical and mesencephalic connections exist with the thalamus, and apparently impulses from the central nervous system may be routed through the hypothalamus to the sympathetic system by these tracts. Thus cerebral cortical stimulation in the postcentral region may produce a fall in the skin temperature of the opposite side, and removal of the cortical area induces a rise in the skin temperature of the contralateral side. The centers for sympathetic regulation lie in the lateral gray area of the spinal cord from the level of the first thoracic to the third or fourth lumbar vertebra.

In 1931 Walter Cannon and coworkers demonstrated secretory activity of the sympathetic system upon stimulation. Apparently a humoral secretion, which they called sympathin and later identified as similar to adrenalin, is produced at the smooth muscle-nerve junction. This secretion, when liberated in the blood stream, elicits similar physiological effects to adrenalin injection. O. Loewi and Sir Henry Dale demonstrated a comparable secretion upon stimulation of the vagus nerve. The agent released acts as a depressor of heart action. Its effect is similar to that produced by injections of dilute solutions of acetylcholine. On the basis of these findings, the terms *cholinergic* and

adrenergic have come into use to designate the actions of parasympathetic and sympathetic components.

Evolution of the Autonomic Nervous System. The parasympathetic division evolved with the cranial and sacral nerves. The protochordates, which show no cranial nerve development comparable with that found in the vertebrates, do not have parasympathetic nerves. All the vertebrates, on the other hand, develop parasympathetic components which accompany cranial nerves 3, 7, 9, and 10.

The sympathetic division is represented in cyclostomes and selachian fishes by segmental fibers emerging with the ventral spinal nerve roots without the formation of sympathetic trunks (Figs. 148, 149). In the dogfish some of these segmental fibers unite in a celiac ganglion and plexus surrounding the base of the celiac axis artery. In bony fishes, amphibians, and reptiles, the segmental nature of the system is further developed with the addition of parallel sympathetic trunks along the celomic wall, lateral to the vertebral column. In birds the distinction between craniosacral and thoracolumbar divisions becomes clear-cut. The cervical sympathetic trunk courses through foramina in the transverse processes of the cervical vertebrae, while in the thorax the trunk is double, one strand passing dorsal and the other ventral to the proximal ends of the ribs. In mammals the system takes on the characteristic features described.

LEVELS OF BEING AND THE NERVOUS SYSTEM

The description of the various brain divisions has concerned itself primarily with structures. The careful reader will have discovered that the nervous system comprises essentially: tracts from the cord to the brain and from the brain to the cord; sensory organs which send their axons to the brain via some of these tracts; correlation and association nuclei whereby the myriad impulses may be resolved in muscular action or thought; and peripheral afferent and efferent nerves representing continuations of the tracts. The question of spontaneous action of the nervous system remains unanswered. Apparently the brain requires stimulation of some kind to think or to react, and recent neurological studies verify the idea that the nervous system is in a constantly disturbed condition, manifested by differences in electrical potential and by passage of electrical waves of varying intensities over the nerve cells and their processes.

The deeper problem, that of the relation of brain to level of being reached by animals and man, and posited by the evolution of the brain and peripheral system, has not been stressed. It must be obvious,

however, that in the absence of a cerebrum, as, to a large extent, in the fish and the amphibians, certain actions cannot take place. It should also be evident that, if the tracts from the spinal cord pass only to higher levels of the cord or stop at the medulla or cerebellum, muscular reactions will be confined largely to these unconscious levels.

Given a cerebrum, we find a great difference in the degree of development in the various vertebrates. A 200-kg. (450-lb.) lion has a brain weight of 263 gm.; a 150-kg. (350-lb.) porpoise has a brain weighing 1,840 gm. This difference is largely in the cerebral weights. Yet no great differences appear in their psychic evolution. Further, it is obvious that genius or idiocy may reside in a 1,200-gm. human brain as easily as in a 2,100-gm. brain. These weight differences alone, therefore, cannot supply the answer to differences in achievement. A certain organization of cerebrum, however, is associated with mental development. Use of language with abstract symbols, ability to reason, awareness of the relations between cause and effect result from this organization. To reach the human level more than brain alone is needed. The space between the mandibles available for the tongue, a free forearm and hand, binocular vision, calcarine brain folds, proper organization and development of the endocrine glands, long learning process—these are factors in placing man at his unique level.

We are accustomed to think of the brain and the nervous system as the executive of the body. The system does control body action within limits; without constant secretions from key endocrine glands, however, the nervous system soon exhibits abnormalities. Parathyroid gland secretion, by its effect on calcium metabolism, and thyroid glands by virtue of thyroxin secretion are but two of the agents that make normal nervous action possible.

Because of countless nerve-muscle connections and the utter dependence of muscle on nerve, the late Dr. Crile and the author were led to an examination of the relation between metabolism and brain size. This study produced startling results in a large series of experiments (489) in which careful metabolism tests were followed by sacrifice of the animal; removal and weighing of the brain showed a constant relation between metabolism and brain size. This relationship indicated that 1 gm. of brain is correlated with 12.15 cal. of heat produced in 24 hours in the habitual temperature range of the animal. This principle held for cold-blooded and warm-blooded vertebrates as well as for many invertebrates. It did not apply to the large-brained primates. The implications of the findings are that a certain brain size appears necessary to achieve the warm-blooded condition; it implies

also that greater continuous-action currents (electrical oscillations) pass from nerve to muscle in warm- than in cold-blooded animals.

Among the Carnivora, ungulates, and primates, those living in the arctic and subarctic generally have larger brains than those in the tropics, and the more active types generally have relatively larger brains than the more sluggish.

TABLE 9. BODY AND BRAIN WEIGHTS

Class	Body weight; kg.	Brain weight, gm.
Carnivora:		
Tiger (<i>Felis tigris</i>).....	160.00	225
Lion (<i>Felis leo</i>).....	190.5	258
Grizzly bear (<i>Ursus horribilis</i>).....	143	234
Polar bear (<i>Thalarchos maritimus</i>).....	200	489
African dog (<i>Canis familiaris</i>).....	14.56	79.99
Collie dog	23.71	84.63
Husky, Canadian	31.75	130.7
Russian wolf (<i>Canis lupus lupus</i>).....	22.68	119
Timber wolf (<i>Canis lubilis</i>).....	29.94	152
Ringed seal (<i>Phoca hispida</i>)	39.76	251
Seal (<i>Phoca richardi geronimensis</i>).....	107	442
Walrus (<i>Odobenus rosmarus</i>).....	79.38	766
Walrus (<i>Odobenus rosmarus</i>).....	667	1,126
Ungulates:		
Barren ground caribou (<i>Rangifer arcticus arcticus</i>).....	128	306
Wart hog (<i>Phacochoerus aethiopicus</i>)..	65	125
Swine (<i>Sus scrofa</i>)....	113	123.9
Coke's hartebeest (<i>Bubalis cokei cokei</i>)..	134	275
Hippopotamus (<i>Hippopotamus amphibius</i>).....	543	540
Cow (<i>Bos taurus</i>).....	408	364
Horse, thoroughbred (<i>Equus caballus</i>)..	531	620
Rhinoceros (<i>Rhinoceros bicornis</i>).....	764	655
Primates:		
Old world monkeys (<i>Macacus rhesus</i>)...	3.63	93.1
Vervet (<i>Cercopithecus aethiops centralis</i>)	4.94	60.7
Red spider monkey (<i>Ateles geoffroyi</i>)...	8.91	102.9
Howling monkey (<i>Alouatta palliata in consonans</i>).....	7.94	53.45
Chimpanzee (<i>Troglodytes niger</i>).....	43.90	325
Man:		
Male Chinese.....	57	1,248
Maya Quiche Indian.....	42	1,270
Male Negro (American)	86	1,265
Male Dane.....	83	1,420

Table 9 shows a few representative vertebrate body and brain weights taken mostly in the field.

Brain-weight differences within a class do not necessarily imply differences in intelligence, although, when classes are compared, changes in cerebrum or other brain divisions are correlated with changes in psychic behavior.

One worker has gone so far as to say that the relatively great weight of the human brain has no special meaning. Recently an anthropologist expressed the notion that the large brain weight in the human being is primarily for balance. It is doubtful whether such a viewpoint will gain much credence in the light of the newer studies of the electrical factors involved in the conduction of impulses and the constant, although variable, electrically excited states of the different parts of the brain. The brain is a part of the energy-releasing system of the body. Through awareness of the ever-changing environmental factors which affect the body and the simultaneous ability to change the relation of the body to these influences, it becomes perhaps the prime translator of energy.

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CHAPTER 7

THE SENSE ORGANS

GENERAL FUNCTIONS

The animal lives in a constant functional relationship with its external environment as well as with its internal parts. As a self-maintaining entity it is equipped with an elaborate array of organs of special and general sense by which it is kept in touch with changes in the world outside and inside. For continued existence in a competitive world it is desirable that the animal project itself beyond the confines of its own body. The special senses represent adaptations to this end. The giraffe that sights the hunter at 2 miles, the impala that scents him at the same distance have successfully projected themselves through this space. Increasing awareness also is written into the specifications of vertebrates as well as invertebrates as they advance to higher structural levels. This increasing awareness is achieved through specialization of a sensory system that enables the animal to see, hear, smell, and feel and to interpret these sensations. Through internal senses the state of the body, its orientation in space, and in warm-blooded animals its regulation of temperature and blood pressure are effected.

The development of sensory organs has been a gradual process both in the invertebrates and vertebrates. In some instances, parallel evolution of the sensory apparatus has occurred in the two divisions. In others, the same ends are achieved by invention of dissimilar systems. The eye of the squid and that of the vertebrate are examples of such parallel development. The acoustic apparatus of the grasshopper and the ear of mammals, the compound eye of insects and the camera eye of vertebrates, on the other hand, are examples of independent evolution in which there is little resemblance between structures with similar functions in widely separate groups. Basic resemblance between the nervous systems of the two leaves little doubt that the vertebrate nervous system was derived from invertebrate ancestry.

The general senses subserve functions of pain, pressure, temperature (heat and cold perception), touch, position, muscle and tendon tonus (proprioceptive), hunger, and sexual activity. Nerve endings are spe-

cific for many of these sensations. Those specialized for pressure are insensitive to temperature, proprioceptive endings are not activated by stimuli which arouse pain in other endings, and so forth. To accomplish specific sensation, receptor endings capable of accepting stimuli, conducting fibers or nerves capable of transmitting them, and a central system capable of appreciating and resolving them into proper actions are necessary.

THE NEUROSENSORY CELL

The simplest type of receptor is the *neurosensory cell* (Fig. 153A). Characteristic of this cell is its position in the covering epithelium.

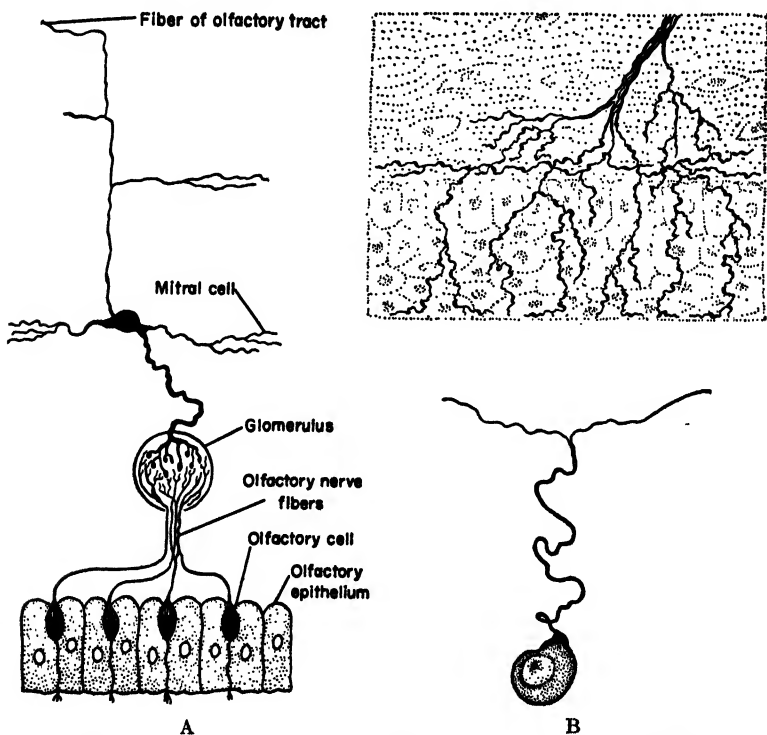


FIG. 153A. Neurosensory cell of the olfactory organ. The cell bodies of neurosensory cells are associated with the olfactory epithelium. Their axons grow into the olfactory bulb and collectively are the olfactory nerve. (After Gray.)
 FIG. 153B. Free nerve endings. These appear in the epidermis, in the epithelium covering certain mucous membranes, and in the papillae of hairs, etc.

Found first in the epithelium of coelenterates, it continues to be represented in the remaining phyla. In annelids and Amphioxus, it is scattered in the covering epithelium; in vertebrates it is retained in the olfactory mucosa. In coelenterates, its axon passes centrally to the musculoepithelial cells and the ganglionic nerve net. In higher invertebrates and chordates, secondary neurons transmit impulses from the neurosensory cells to the central nervous system. In its primitive state, it probably transmits various types of sensations; in the olfactory epithelium, it accepts chemical stimulation from gases in solution in the air; in fishes and Amphibia, it responds to solutions in liquids. In land animals, this last function is partly taken over by the sensation of taste.

FREE NERVE ENDINGS

A second type of sensory cell, probably derived from the first, is the *free nerve ending* (Fig. 153B). Cells of this type no longer lie in the surface epithelium, but their dendrites arborize and anastomose in the subcutaneous and the deep layer of the skin, while the cell body has receded into the deeper subcutaneous tissue. Axons pass centrally from the cell bodies and transmit the stimuli to the central system. These cells accept and transmit pain and pressure sensations. The free endings may extend into the germinative and granular layers of the epidermis. Such endings are also found in the mucous and serous membranes, the walls of blood vessels, the cornea, teeth, and periosteum.

SECONDARY SENSORY CELLS

Besides cells with free endings, various types of specialized end organs occur in the skin, mucous membranes, articulations, muscles, and tendons. These have in common a connective-tissue capsule enclosing the naked axis cylinder of the nerve cell. We recognize three types of such endings, *bulbous*, *lamellated*, and *oval corpuscles*.

Bulbous corpuscles, also called the end bulbs of Krause, are minute oval bodies with thin capsules derived from the epineurial connective tissue (Fig. 154). They contain a semifluid core into which passes the axis cylinder. The latter terminates in a bulbous or plexiform enlargement. They occur in the conjunctiva, mucous membranes of the mouth and nasal cavity, penis, and clitoris. They appear in all vertebrate classes, transmitting both cold and tactile sensations. Modifications are the Golgi-Mazzoni bodies in the skin, associated with pressure, and the Grandry corpuscles in the tongues and beaks of birds.

The lamellated corpuscles, also known as pacinian corpuscles, consist of a capsule of several layers, or lamellae, surrounding the naked

axis cylinder in a central clear space within the capsule (Fig. 154). They are distributed to the deeper parts of the body, to the skin, in the areolar tissues of joints, and along certain nerves. The single nerve fiber ends in a knob-like enlargement. Modifications are the Herbst corpuscles in the feather follicles and the skin of the beak of the duck and perhaps other birds.

In the oval corpuscles, also called the Wagner-Meissner corpuscles, the connective-tissue capsule is pierced by the axis cylinder after it spirals around the capsule (Fig. 154). The naked end fiber terminates in small, pear-shaped enlargements. It is found in the corium of the

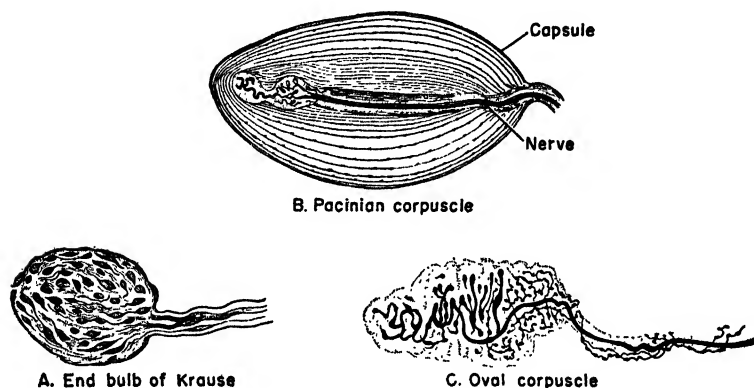
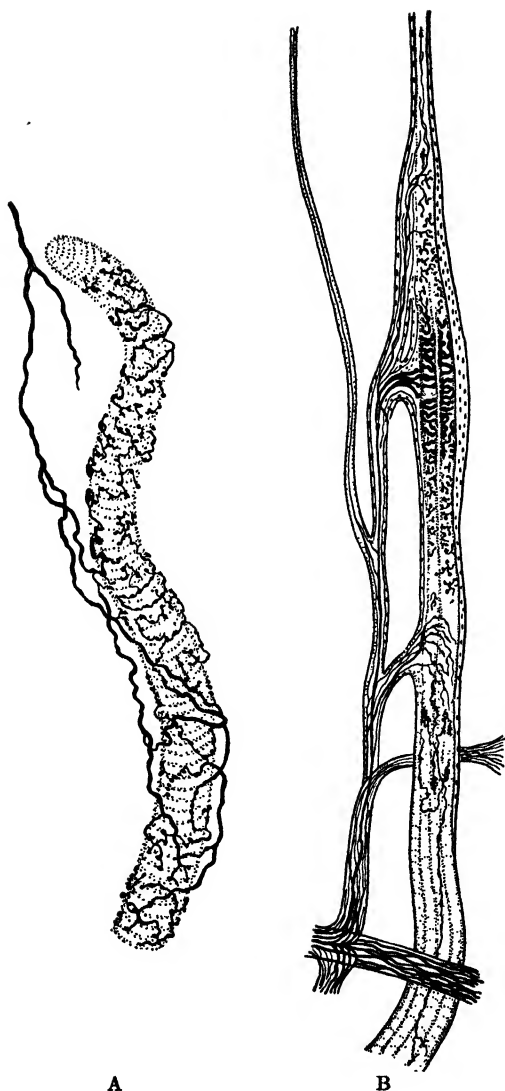


FIG. 154. Special end organs. A, end bulb of Krause. B, pacinian corpuscle with several capsules. Arterioles pass into the central capsule; the nerve ends in a slight enlargement. C, oval corpuscle; the nerve spirals around the corpuscle and ends in small nodular enlargements.

hand, foot, and forearm, mucous membrane at the tip of the tongue, skin of the lips, and skin of mammary papillae. Modifications are the Merkel corpuscles, particularly well-developed in the skin of the pig's snout, and the corpuscles of Ruffini, in the subcutaneous tissues of the fingers. While tactile in function, the corpuscles in modified form transmit pressure and warmth. The Meissner corpuscles, which belong to this group, are confined to the Primates.

Sensory nerve endings, known as neuromuscular and neurotendinous spindles, appear in voluntary muscles and in tendons (Fig. 155A and B). These may be simple, naked interstitial endings in muscle, which, by repeated divisions, distribute themselves to the intermuscular connective tissue. Specialized endings also occur in the muscles, where



A

B

FIG. 155A. Neurotendinous spindle. These endings are frequently associated with tendon-muscle junctions. (After Dogiel.)

FIG. 155B. Neuromuscular spindle. These spindles consist of embryonic muscle tissue, covered by a capsule. The sensory nerve fiber terminates within the capsule.

the latter retain an embryonic appearance. Surrounded by a capsule, the nerve fiber penetrates this, loses its sheath, and terminates in the core. Neurotendinous fibers at the muscle-tendon junctions are surrounded by a capsule, while the nerve fibers enter as they do in the neuromuscle spindles. The nerve fibers terminate in discs or in plexiform enlargements.

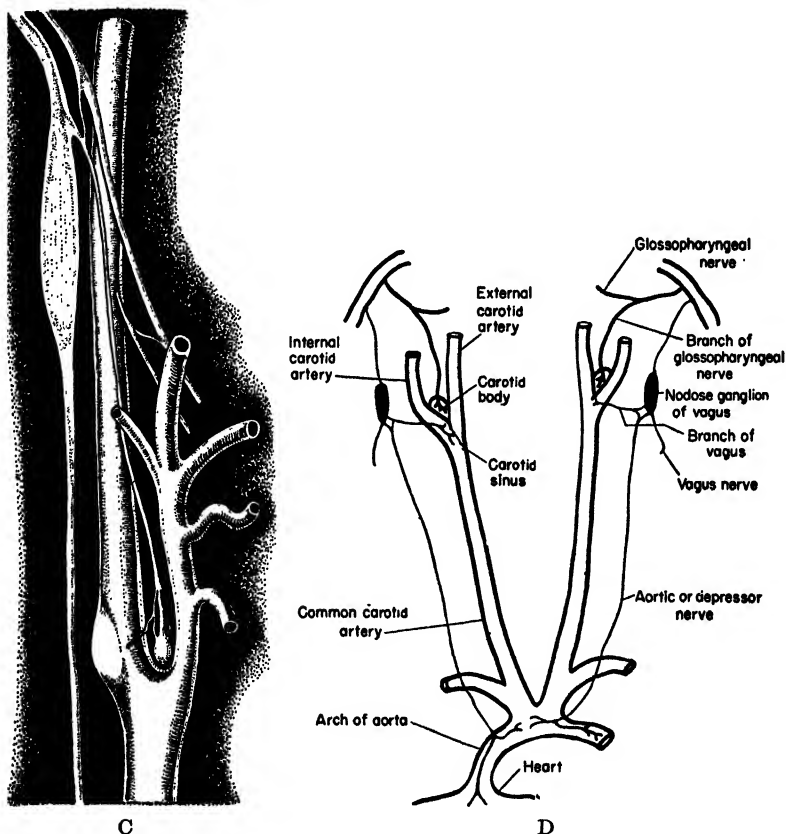


FIG. 155C and D. Carotid sinus and glomus aorticum. The sinus is a small enlargement at the origin of the internal carotid artery. Afferent nerve fibers pass to the ninth cranial nerve. The glomus lies at the junction of the external and internal carotid arteries. Nerve fibers from the glomus also join the glossopharyngeal and the vagus nerves. (C, after Cunningham; D, after Ranson and Clark.)

These neuromuscular sensory endings must not be confused with the endings of the motor nerves, which are of two general types (Fig. 155). One, the nonmedullated autonomic nerve fibers without specialized endings, is found in smooth muscle. The nerve fiber arborizes near its termination to form plexuses; from the plexuses delicate fibrillae pass to the region of the muscle nuclei and end in slight swellings. The other type terminates in motor end plates. Medullated nerve fibers to the muscle form plexuses in the perimysium by division into nerve filaments. In this way each muscle fiber eventually receives its own innervation. As the nerve approaches the muscle fiber, it loses its myelin sheath and ends within the sarcolemma in a granular layer of clear muscular nuclei and Schwann's cells, to form the motor end plate.

Other specialized nerve sensory endings are placed at the junction of the external and internal carotid arteries in the carotid sinus and in the aortic arch as aortic receptors (Fig. 155C). These endings, sensitive to pressure changes within these vessels, increase and decrease blood pressure through a reflex which involves the glossopharyngeal and vagus nerves and the medulla oblongata. A branch of the glossopharyngeal, designated the sinus nerve, supplies the carotid sinus; the depressor nerve, a branch of the vagus, transmits impulses from the endings on the aortic arch. In the rabbit the depressor nerve arises high in the neck from the vagus; in the dog, on the other hand, depressor fibers extend in the vagal trunk descending to the heart. Closely associated with the carotid sinus and aortic receptor are specialized chemoreceptors. These are a carotid body at the junction of external and internal carotid arteries, supplied by the glossopharyngeal nerve, and aortic bodies associated with the bases of the subclavian arteries, supplied by the vagus nerve. They act as regulators of respiration. As chemoreceptors they respond to variations in the carbon dioxide concentration in the blood and, acting on the respiratory centers in the medulla, affect the rate of breathing. Their action must not be confused with the action of the carotid sinus.

THE LATERAL LINE SYSTEM

The lateral line system of cyclostomes, fishes, and aquatic amphibians is a system of superficial channels in the skin, along the dorso-lateral aspect of the body and the supra- and infraorbital, mandibular, and hyomandibular canals in the head region (Fig. 156). These channels are retained in the epidermis of cyclostomes. In fishes and amphibians they lie more deeply and communicate with the surface by pores spaced at varying intervals. Their innervation passes to sensory

areas in the epithelium of the channels. The system is derived from *neuromast sensory cells* scattered over the body surface. In the integument of the head of the elasmobranch fishes are other sensory aggregates, the *ampullae of Lorenzini* (Fig. 156C). These ampullae are individual neuromast cells which have receded from the surface but which retain connections with it through small pores. A tube passes internally from the pore, and at its base is an oval-shaped sensory ending. A modification of this type is the *ampulla of Savi*, found in Torpedo. These differ from the Lorenzini ampullae since they are

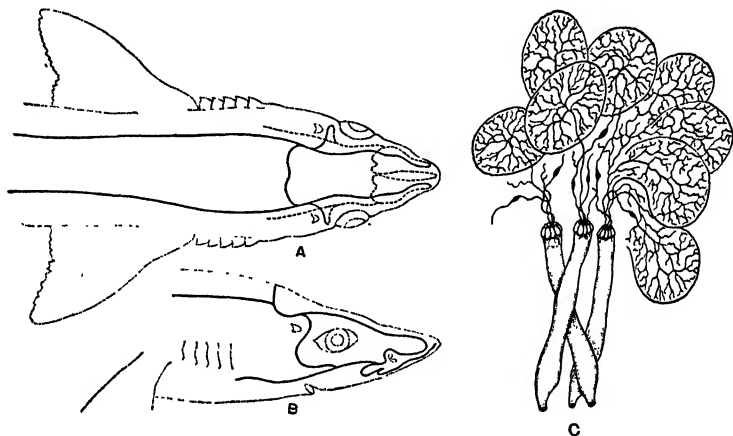


FIG. 156. The lateral line system. A, dorsal view. B, lateral view. The system is a line of canals with sense organs known as neuromasts supplied by the seventh and tenth cranial nerves. It is limited to fishes and aquatic amphibians. C, ampullae of Lorenzini. These are small bulbar enlargements marking the termini of the canals of Lorenzini. The bulbs are under the skin surface, upon which they open by pores. They are supplied by delicate sensory-nerve fibers.

completely closed off from the surface. They are covered by a single layer of epithelium under which lies the sensory cell. The lateral line system and the ampullae are innervated by somatic branches of the facial, glossopharyngeal, and vagal nerves. It responds to current and pressure changes and probably accepts vibrations of low intensity.

THE SPECIAL SENSES

Included in the special senses are smell, taste, sight, and hearing. The first two apparently are universal in the chordates; the last two are not so generally represented. Thus sight, by which we refer to the

production of definite images, and hearing are absent in the protochordates. Sight is developed in all vertebrate classes but not in all species; hearing, on the other hand, through a definite acoustic apparatus associated with the balancing organ, does not occur below the amphibian level, although fishes are able to perceive sound by development of an air vesicle associated with the swim bladder and the internal ear.

It is difficult to imagine chordate or, for that matter, invertebrate development proceeding to its present high state without the appearance of special senses. This does not require the invoking of the doctrine of need. We may say that the special and general senses were basic to the success of organisms, as we find them today. It is stated occasionally that we and perhaps other animals possess senses which have not yet been analyzed or localized or for which a physical basis may only be assumed. Attempts have been made to explain clairvoyance, mental telepathy, and so-called extrasensory perception by evoking such functions. While the emergence and acquisition of new forms of perception are not ruled out of present-day animal organization, at present we have no structural or physiological evidence to indicate a physical basis for these alleged phenomena.

The Olfactory Organs. Smell is a chemical sense, in contrast to hearing, which depends on both physical and chemical factors. In land animals smell is stimulated by gaseous, while taste acts in aqueous, solutions. Particles may be much more diffuse to stimulate the olfactory endings than to initiate taste impulses, although, to excite either, particles first pass into solution. In gill-breathing aquatic animals a rigid distinction between the two senses breaks down, since the animal is able to smell liquid solutions, and even in our own case the two senses are closely linked in function. The primary olfactory functions are associated with food getting, discrimination between edible and inedible substances, and with protection. Smell has transcended its original function and is a warning device against enemies and a means of recognizing friends; it is active also as a sexual excitant.

The olfactory organ is closely related to the surface of the body. In *Amphioxus* and in the cyclostomes it is confined to a single groove or pit; in other vertebrates the olfactory organ is paired. Bipolar olfactory cells distributed in a supporting olfactory epithelium retain a primitive character closely akin to neurosensory cells. A delicate superficial process, the olfactory hair, passes to the surface, while a deep, nonmedullated extension, the axon, runs proximally and collectively represents the olfactory nerve. The olfactory nerves pass through the anterior-ventral floor of the skull or cribriform plate and enter the olfactory bulb. In the

bulb they effect synapses with mitral cells whose axons become the fibers of the olfactory tract. The tracts from the right and left olfactory organs pass to the rhinencephalon, or olfactory brain.

Beneath the olfactory epithelium of land animals, and constituting the deep layer of the mucous membrane, are the *glands of Bowman*, serous in nature. They maintain a moist surface and an equable temperature in the olfactory organ of mammals. The olfactory epithelium is ciliated, thus clearing debris and secretions from the surface and providing for a constant sensitivity to particles whose flavors are to be tested by the sensitive cells.

In *Amphioxus* the olfactory organ is associated with the *neuropore* as an epithelial invagination. With closure of the neuropore during development the olfactory epithelium is limited to a depression at the site of the original opening. This depression moves to the left of the midline. In cyclostomes the *olfactory pit* develops at the site of the neuropore but does not appear until after its closure. Through cell proliferation the pit becomes associated with the hypophysis, and in the adult *Petromyzon* this connection is retained. In the myxinoids the hypophysis acquires, in addition, a connection with the foregut, and thus a direct channel extends from the external nasal opening to the gut by way of the hypophysis. The olfactory epithelium in cyclostomes carries cilia and sensory hairs, which are retained in the remaining vertebrates. An approach to the paired olfactory organs is made in the cyclostomes through paired olfactory nerves.

In fishes, paired olfactory organs anterior and commonly dorsal to the mouth are guarded by skin flaps. In some elasmobranchs, a superficial groove connects the organ with the mouth. In dipnoan fishes, the olfactory pit opens inside the upper lips, foreshadowing the *narial canal* in the amniotes. In the latter, with appearance of maxillary or palatine folds and plates, which in mammals fuse to form the hard palate, a *nasopharyngeal duct* unites *external* with *internal choanae*. The palatal ridges do not join in reptiles and birds, but a membrane, the soft palate, extends between and beyond them. With appearance of an external nose a *vestibule* is added to the olfactory organ, and the olfactory epithelium is restricted to an area between the vestibule and the nasopharyngeal duct. Ethmoidal and maxillary *conchae*, extensions of ethmoid and maxillary bones arranged in turbinate form, offer a broad surface for the olfactory and respiratory epithelium (Fig. 157). The conchae and their covering epithelium are outpocketings of the nasopharyngeal duct.

Sinuses in the frontal, ethmoidal, sphenoidal, and maxillary bones, lined with secretory epithelium, communicate with the nasopharyngeal

canal (Fig. 157). Their alleged function is to reduce the weight of the skull and to serve as resonating and perhaps as warming chambers.

A further structure associated with the olfactory apparatus of land vertebrates is *Jacobson's organ*, present in many amphibians and reptiles, in monotremes and marsupials, and in some placental mammals as an outpocketing in the nasopharynx, covered with olfactory epithelium. In mammals it communicates with the mouth cavity by a duct through the incisive foramen. It receives secretions from the serous glands of the nose and from the lacrimal glands; thus its olfactory surface is bathed

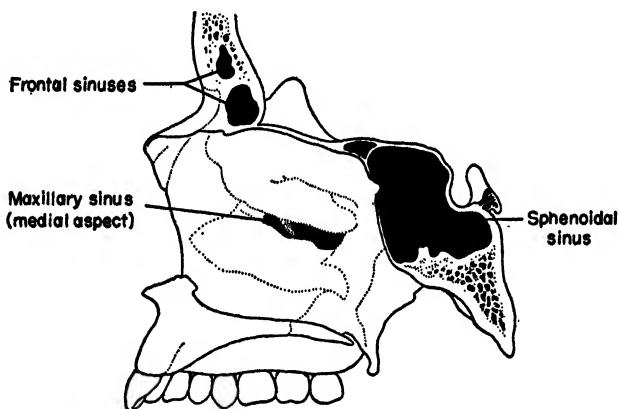


FIG. 157. Skull sinuses. Various explanations are offered for the presence of skull sinuses, such as reduction of weight, resonance, and warming of inspired air. The sinuses are lined with ciliated epithelium and open into the nasopharynx.

with fluid, a condition comparable with that in aquatic vertebrates, where the olfactory epithelium is constantly bathed by water. It has been considered, consequently, a remnant of the original olfactory organ which has retained its primitive condition.

Taste Organs. The presence of taste organs in aquatic chordates apparently depends on the fact that the habitat of these animals contains varying amounts of dissolved substances, some of which imply the presence of food; others indicate noxious or toxic agents. The presence of taste organs on the surface of head, body, and fins, in the mouth and pharynx of fish, indicates their employment as water-testing device. In land animals, taste organs are restricted to the tongue, soft palate, epiglottis, pharynx, and upper part of the larynx. They function in

aqueous solutions as they do in the fishes, except that only small samples are presented to them for testing. In contrast, as noted, olfactory organs in land forms respond to gaseous mixtures.

Taste cells are flask-like aggregates of modified epithelial cells called taste buds (Fig. 158). The supporting cells of the bud form an enclosure with a wide bottom and a tapered neck. Within the enclosure are neuro-epithelial taste cells. The entire capsule has commonly retreated from the surface and lies in the epithelium. The tapered free end of the capsule terminates in a sunken pit and communicates with the surface by

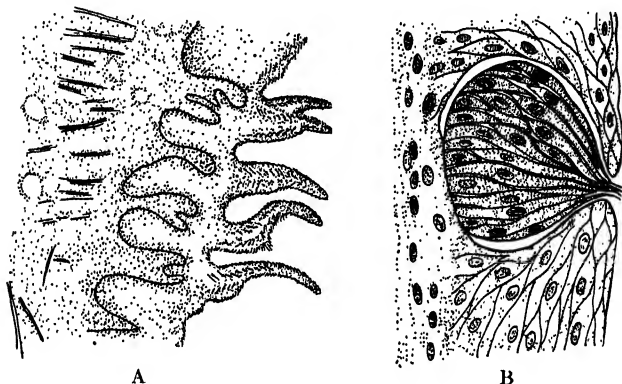


FIG. 158. Taste papillae. These are special nerve endings of various types, associated with tongue and pharynx and in some fishes with the surface of the body. *A*, filiform papillae cover the anterior surface of the tongue; fungiform are projected onto the surface by a stalk. *B*, vallate are sunk into the surface and are surrounded by a moat; foliate are arranged in folds along the margins of the tongue.

a taste pore. A taste hair from the taste cell protrudes into the lumen of the pit. From 4 to 20 taste cells occur in a taste bud.

The buds generally are found in specialized papillae developed from the corium and according to their shape are called *filiform*, *fungiform*, *vallate* (circumvallate), and *foliate*. The filiform are distributed over the anterior two-thirds of the tongue surface. They have a hard connective-tissue core with branched papillae. The covering epithelium of bristle-like processes in carnivores results in the brush-like, rasping surface of the tongue. The fungiform papillae have a stalk projecting from the corium and a rounded top in which are secondary papillae. The vallate papillae do not project from the tongue surface but are sunk into it, each surrounded by a circular moat or groove from which the papilla projects

like an inverted cone with the taste buds in the lateral surface. From 8 to 12 vallate papillae are arranged in an open V with the apex directed posteriorly at the level of the foramen caecum, on the dorsum of the human tongue. Foliate papillae are oval bulgings with deep grooves at their sides on the mucous membrane of the lateral part of the posterior tongue surface. Plentiful in the rabbit, they are but rudimentary in man. Filiform and fungiform papillae also contain tactile and cold-perceiving nerve endings. Nerve cells, after having lost their sheaths, penetrate the taste buds and end between the taste cells. Taste is not entirely restricted to these specialized endings but may be perceived by fibers in a subepithelial plexus formed by arborizations from the chorda tympani branch of the facial and lingual branches of the glossopharyngeal nerves. The former supplies the anterior two-thirds of the tongue surface and the latter the posterior one-third.

Mammals are better supplied with taste buds than are birds or reptiles. In the latter, some 300 occur on the tongue, while in mammals they are numbered by the thousand. Circumvallate papillae decrease in number during life. In an infant there are about 245; in an adult, 208; in extreme old age, about 88.

The Eye. The eye is in many respects the most highly refined of all the sense organs in many vertebrates. While smell, particularly in the Carnivora and the ungulates, is stimulated by dilutions of the order of one part of the gaseous substance to billions of parts of air, neither smell nor any of the remaining senses have the amazing qualities of sight. The formation of images on a sensitive screen, the transmission of these images in orderly fashion to interpreting and storing centers in the brain, the ability to recall these images years after their impression—all these are involved in seeing: the entire mechanism of sight remains one of the most improbable structures in a highly improbable body.

Eyes have a long heritage. A few simple experiments with Protozoa indicate that protoplasm, in the absence of special senses, responds to light. The reactions to optimum intensities are positive; to very intense light they are generally negative. With the appearance of neurosensory cells in the coelenterates, sensory functions start on their long road to specialization. Higher invertebrates have evolved two types of eyes, the camera eye of the squid, which parallels in structure the vertebrate eye, and the compound eye of the arthropods, in which multiple facets, lens, and retinal cells appear. The vertebrate eye, therefore, while it may be an independent invention, was foreshadowed some 300 million years earlier in the eye of the squid and had an analogue in the insect eye.

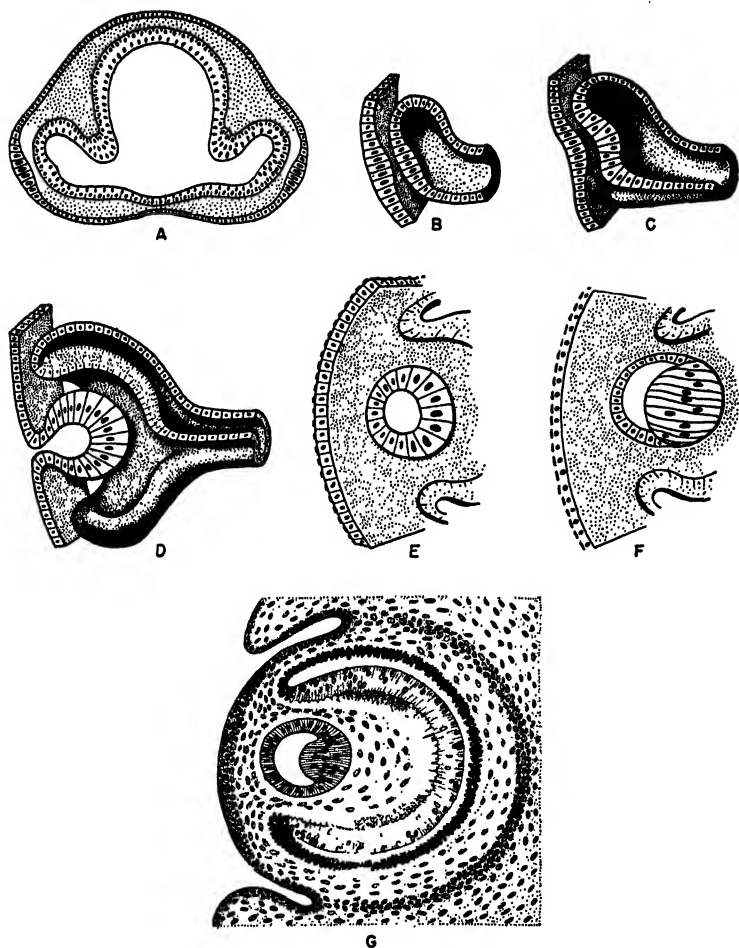


FIG. 159. Development of the eye. A, evagination of the brain wall and thickening of the ectoderm; B, approximation of brain tissue to wall and constriction of evaginated portion; C, beginning of formation of optic cup; D, invagination of ectoderm to form lens and envelopment by optic cup; E, F, lens has been pinched off from ectoderm and is becoming enfolded by optic cup; G, differentiation of nervous and pigmented retinal layers. The dark cellular layer represents the future retina. (G, after Kollmann.)

The chordate eye did not spring full-fledged from the hands of the gods as an image-perceiving organ. In common with the rest of the body it had a relatively simple beginning and today is observed at different levels of performance in various chordate classes. In *Amphioxus*, retinal or sensitive cells occur as part of the central nervous system. These eyes are not homologous with those of higher vertebrates. The "eye" of *Amphioxus* consists of a sensory and a pigment cell. The latter surrounds the eye like a beaker, while from the sensory cell an axon extends to and links it with the central nervous system. Light enters the base of the cell opposite the point of emergence of this process. It presents therefore the same inverted characteristic of the vertebrate eye, in which light strikes the basal layer of the retina before affecting the rods and cones. Such cells in *Amphioxus* are scattered along the spinal cord. Another pigmented spot lies on the brain wall in a position homologous with that of the vertebrate eye. This spot, however, is insensitive to light.

In vertebrates, paired eyes arise with the transformation of the neural plate into the neural tube (Fig. 159). Invaginations, called *optic pits*, appear in the neural plate, at the site of the future *optic vesicles*. The vesicles are constricted where they attach to the forebrain. These constrictions form the *optic stalks*. By indentation of the optic vesicles they are converted into two layered *optic cups*. The cup is incomplete at one margin; this opening represents an embryonic *chorioid fissure* through which the hyaloid artery supplies the developing eye and through which mesenchymatous tissue enters to form the aqueous humor and vitreous body. In the adult the fissure and the artery are obliterated. With transformation of the vesicle the surface ectoderm opposite the optic cup becomes thickened to a *lens placode* and invaginates. This invaginated part, not to be confused with the earlier invaginated optic pits, separates from the surface to form the hollow spherical *lens vesicle*, which approaches the lips of the optic cup and eventually lies within its cavity. The cells of its posterior wall lengthen and are converted to *lens fibers*, which grow forward and obliterate the original hollow lens vesicle. The anterior lens wall retains its cellular character in the epithelium on its anterior surface.

Retina. After its conversion from an optic vesicle to a two-layered optic cup, further differentiation in the inner layer occurs, while the outer becomes pigmented and remains a single-celled columnar epithelium (Fig. 160). The latter is the *pigmented epithelial layer* of the retina. The inner layer becomes the highly specialized nervous division of the

retina, separated, beginning with its inner surface adjacent to the vitreous humor, into the following strata:

1. Ganglionic layer
2. Inner plexiform layer
3. Inner nucleated layer (inner granular layer)
4. Outer plexiform layer
5. Outer nucleated layer (outer granular layer)
6. Layer of rods and cones

The rods and cones lie adjacent to the pigmented epithelial layer, and they point away from the source of light. In other words, the light must

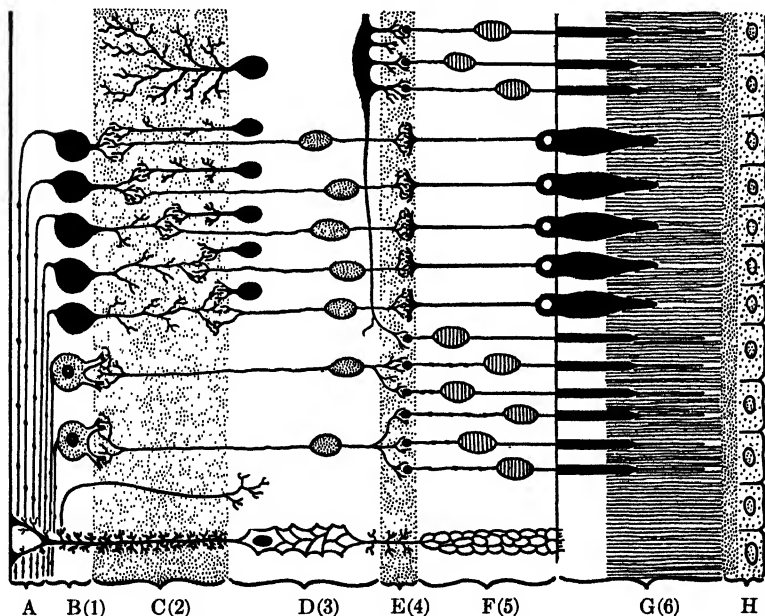


FIG. 160. The six layers of the retina and the stratum opticum. A, stratum opticum; B, ganglionic layer; C, inner plexiform layer; D, inner nucleated layer; E, outer plexiform layer; F, outer nucleated layer; G, layer of rods and cones. H, pigmented layer. (After Cajal.)

pass through the remaining retinal layers before striking the rods and cones. Beginning with the layer of rods and cones, a limiting membrane partly separates them (6) from their nuclei (5). Rods and cones are processes of the visual cells whose nuclei represent layer 5. Cones are

more sensitive to color, rods to low light intensities. A limiting membrane between the inner ends of the rods and cones and the outer nucleus layer serves as a support to maintain the former in a perpendicular position. The rod and cone nuclei (5) are arranged in several rows, apparently to accommodate them, since their bulk is greater than that of the rods and cones.

An outer plexiform layer (4) represents the synaptic junctions which the axons of the rods and cones make with the dendrites of the bipolar cells of the inner nuclear layer (3). A peculiarity of these synapses is that one dendrite of the bipolar cells may make contacts with a number of rod and cone processes. In primates some of the cones make connections with individual bipolar cells. Such cells are called midget bipolars, in contrast to the diffuse bipolars whose processes embrace a number of rod and cone axons. The cell bodies of these bipolar cells, as indicated, form the inner nuclear layer (3), while an inner plexiform layer (2) results from the synapses between the axons of these bipolar cells and the dendrites of the ganglion cells (1). The latter constitute the innermost cell layer of the retina. This ganglion stratum consists of cell bodies whose outer processes, as indicated, synapse with axons of bipolar cells (2) and whose inner processes or axons pass along the vitreous margin of the retina. These inner processes, or axons, are sometimes designated as the stratum opticum, the inner surface of which is covered by an internal limiting membrane. They are directed to the *fundus* of the eye and collectively are the optic nerve, which traverses the retina at the "blind spot" as well as the chorioid and sclera in its passage to the floor of the diencephalon.

Horizontal and amacrine cells are other components of the retina. Assumed to have conducting functions, they are extremely numerous in birds, where, according to Walls, they may outnumber the bipolar neurons. Müller's fibers and neuroglia are the supporting cells of the retina. They fill in the spaces and support and insulate the nerve fibers.

The retina receives nourishment through the *chorioid coat*, which surrounds the pigmented layer of retinal cells and is of mesenchymatous origin. The blood reaches the chorioid by long and short ciliary branches of the ophthalmic artery and is drained from the eye by small veins which open into four larger vorticosae veins. According to Walls, only mammals and eels possess vessels which invade the retina itself. In man a very small central retinal artery and vein traverse the center of the optic nerve to the retina. This small artery is also a branch of the ophthalmic artery.

Sclera and Cornea. The true supporting structures for the eyeball are

the sclera and the cornea, which together constitute the fibrous tunic of the eyeball, (Fig. 161A). The sclera is the opaque, outer, tough, tendinous layer of the eyeball. It is a closely interwoven, felted connective tissue of mesodermal origin. In a 90,000-lb. humpback whale the eyeball had a diameter (horizontal) of $3\frac{1}{4}$ in., of which $2\frac{1}{8}$ in. was accounted for by the scleral wall.

Anteriorly the cornea is a continuation of the sclera, but in contrast to the opacity of the latter the cornea is transparent. It does not contain blood vessels and depends upon lacrimal fluid for its nourishment. The junction of cornea and sclera is the rim, or *limbus*, of the cornea. The

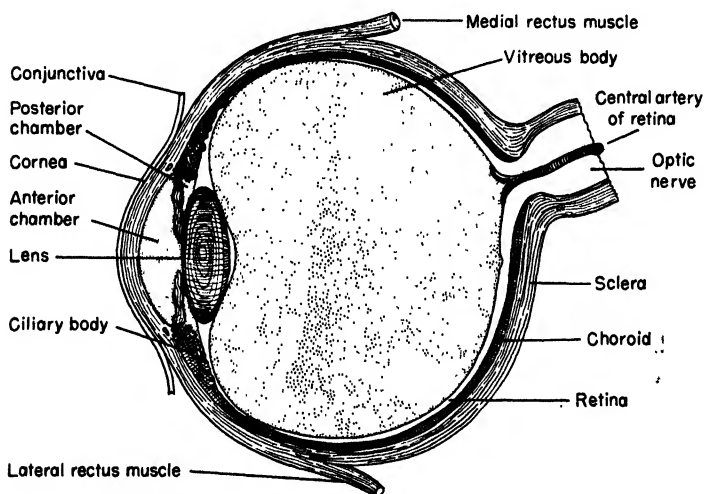


FIG. 161A. Section through adult eye.

cornea is covered by an epithelial layer of the skin, the *conjunctiva*, which lines the deep surface of the eyelids and is reflected from these over the front of the eye. Under the eyelids it is vascular, but it thins out over the corneal surface and becomes transparent and without blood vessels. The cornea carries pain and other sensory nerve endings.

Uvea. The inner surface of the sclera is lined by the heavily pigmented chorioid, not to be confused with the pigmented layer of the retina. This coat is also known as the uvea, or uveal tract. It is a connective tissue in which a rich vascular network, derived from the long and short ciliary arteries, ramifies. It is the source of nourishment for the retina, sclera, and other structures of the eye. The retina lines the

uvea and at its circumference forms the ora serrata. Anterior to the ora the chorioid is modified to become the ciliary body, largely of meridional and circular smooth muscle fibers and blood vessels. The muscle fibers are used largely in accommodation by changing the convexity of the lens. Finger-like extensions of the chorioid layer, near its junction with the iris and caused by its infolding, result in a ring of ciliary processes where its surface approximates the lens.

Iris. The iris is a thin contractile disc perforated at its center by the pupil and continuous peripherally with the ciliary body. It contains a

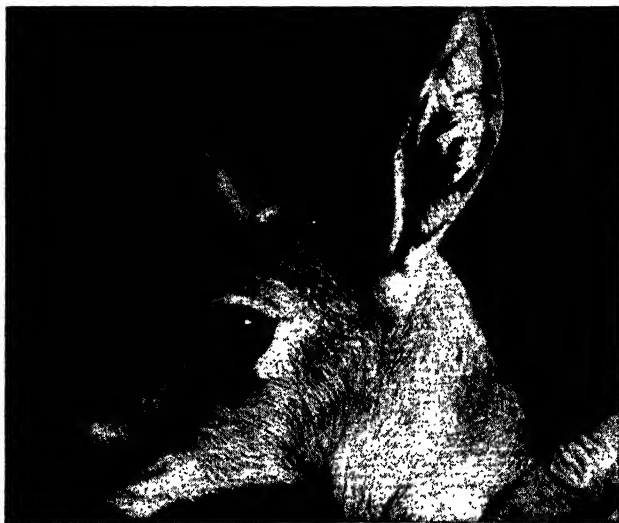


FIG. 161B. The eye of Thomson's gazelle.

ring of circular smooth muscles, the sphincter pupillae, and a radially arranged contractile myoid lamina, the dilatator pupillae. The last is not a true smooth muscle layer but consists of contractile epithelial cells. Eye color is due to the amount, nature, and dispersion of pigment granules in this coat. In brown eyes the melanin pigment is distributed to both the inside and the front layer of the iris; in blue eyes the colorless granules are confined to the inside layer, and the color is produced by light reflection from the translucent layer; in albino eyes pigment granules are absent. The *pupil* is the circular opening in the iris. Its aperture varies in the normal eye inversely to the intensity of the external light and is regulated by the sphincter and dilatator pupillae.

The iris divides the space between the cornea and the lens into (1)

an anterior chamber bounded by the inner margin of the cornea and outer surface of the iris, (2) the posterior chamber between the inner surface of the iris and the zonule fibers connecting the lens and the ciliary body, and (3) the chamber of the vitreous humor in the fundus of the eye, bounded by the retina and the posterior surface of the lens.

Anterior and posterior chambers are filled and kept distended by the *aqueous humor* secreted by the ciliary epithelium covering the ciliary processes. It is about 98 per cent water and 1.4 per cent sodium chloride. Excessive secretion is removed by the capillary network. In cyclostomes and fishes a secreting mechanism is absent, and presumably the aqueous humor is acquired by osmosis. The *vitreous humor*, secreted by mesenchymatous cells during development, is not constantly renewed as is the aqueous. Hence loss of the vitreous is more serious; it may be replaced by aqueous humor after ocular injury.

The Eye in the Vertebrate Classes. The following account of the eye in the vertebrate classes is based largely on the excellent description of the vertebrate eye by Walls, who has performed a herculean task in gathering and interpreting the present knowledge of the vertebrate eye.

The lamprey eye is the simplest of the vertebrate eyes. Outstanding features are: (1) the innervation of inferior and external rectus muscles by the abducent nerve; in other vertebrates the external rectus is supplied by the abducent, while the inferior rectus receives a branch from the oculomotor nerve; (2) the attachment of the superior oblique muscle to the ventrotemporal quadrant of the eyeball; (3) a cornealis muscle caudal to the eye and attached to the margin of the cornea; (4) a special skin thickening over the cornea, called the spectacle, to which the cornealis muscle actually attaches. Upon contraction the spectacle is drawn taut and flattens the cornea. The cornea is a thin structure; ciliary body and zonule fibers are absent; the lens is spherical, and ganglion cells of the retina are intermingled with the inner nuclear layer; primitive ependymal cells, corresponding to those of the lining of the brain, lie in the center of the optic nerve. In hagfishes and myxinooids the eye is vestigial and nonfunctional; lens and eye muscles are absent, and there is no differentiation between sclera and chorioid.

Outstanding elasmobranch characteristics are: a nictitating membrane; an optic pedicel, which is a small, cartilaginous supporting rod resting against the cranium with an expanded cup-like portion articulating with the eyeball; a thick sclera, the lens held in place by a suspensory ligament; beginnings of sphincter and dilatator muscles in the iris. The visual cells of the retina, with some exceptions, consist of rods only.

The teleost eye may have temporary lids moved by a special dermal

muscle, while adipose lids occur in certain swift swimmers. A tentacular eye-supporting ligament is found in some species. The eye muscles are frequently long and are carried to the eyeball through canals in the bones of the skull. The eyeball is flattened at its outer free surface; the sclera usually contains cartilage but may be entirely bony; an annular ligament joins the cornea with the iris. The chorioid layer contains a chorioid gland which is a plexus of blood vessels. Projecting into the vitreous cavity a falciform process forms a ridge of pigmented and vascular chorioidal tissue. Hyaloid vessels may occur on the inner retinal surface. A retractor lentis muscle extends from the margin of the falciform process and is attached to the lens capsule; a suspensory ligament also connects with the lens margins. A tensor chorioidea muscle lies in the ciliary zone of the chorioid. The iris contains a sphincter muscle. The retina varies in thickness from 100 to 500 microns; guanine occurs in the retina of some fishes. In addition to ordinary rods and cones, twin cones are common. Their presence is associated with exposure to bright light. Some deep-sea fishes have only rods in the visual layer of the retina.

In Amphibia the cornea is directly exposed to the air and "becomes an important refractive surface. With some of the burden of focussing the image on the retina taken from the lens, the latter now recedes behind the iris. The pupil has gained in mobility; the lens is brought into the plane of the ciliary body; it becomes possible to discard the lens-moving muscles and instead use the ciliary muscles for accommodation."¹ Amphibia do not have fully developed eyelids as one might expect in a land form, but a nictitating membrane is a partial answer to the demands for protection, while harderian glands furnish lubrication for the eye.

The retina in the Anura has single and double cones and red and green rods. In some species the cones contain oil droplets. The ciliary body is poorly developed. A retractor bulbi surrounds the optic nerve and attaches to the eyeball. This is a feature common to the tetrapods, with the exception of certain reptiles and the Primates. A protractor lentis attaches to the lens capsule, and upon its contraction the lens is pulled away from the retina. The ciliary muscles are discontinuous.

In the reptiles a number of new features are added to the eye that concern chiefly the method of accommodation by a lens-squeezing mechanism effected by the striated ciliary muscle fixed to the rim of the cornea. The lens is less viscous than in other forms, and contraction of the ciliary muscle causes it to bulge into the cavity of the anterior

¹ Walls, G. L., *The Vertebrate Eye*, *Cranbrook Institute of Science Bulletin* 19, p. 592, Bloomfield Hills, Mich., 1942.

chamber. The inner layer of the retina in some reptilian groups is nourished by a *conus papillaris*, a conical projection from the head of the optic nerve. Earlier reptiles possessed a pure cone, or diurnal type of visual cell; in the later forms, with the exception of the snakes, rods are added, and in some only rods occur. It will be remembered that rods are sense receptors for light of low intensity and without color, while cones are adapted for light of high intensity and for color sensation.

Turtles generally possess diurnal eyes, *i.e.*, adapted for bright light. The sclera is cartilaginous with added bony ossicles. The cornea is thick, and the lens is the softest among vertebrate eyes. Cones predominate, but there are some rod-like cells in the visual layer of the retina. Crocodiles in contrast have nocturnal eyes. A *conus papillaris* is lacking, as it is in the turtles. Snakes exhibit some peculiar characteristics in their optic architecture. The sclera is entirely tendinous; melanophore cells occur in its outer surface. The chorioid is extremely thin, consisting largely of a *choriopapillaris*. The muscles of the iris are striated, their fibers arranged primarily in two circular bands, one near the margin of the pupil called the *sphincter pupillae*, the other near the corneal-scleral junction. The lens is quite firm. A plexus of blood vessels lies on the inner retinal surface, but hyaloid vessels also occur. Both rods and cones are found in the visual layer.

Birds and reptiles show many common eye features (Fig. 164). Perhaps the chief distinguishing characteristic of the former is the large size of the eyes, in some cases exceeding the brain in weight, and the presence of a pecten. The ostrich has the largest eye of the land vertebrates. It is about 50 mm. in diameter; hawks and owls, with a fraction of human body weight, have eyes as large as or larger than man. The eyes contain a prominent concavity at the corneal-scleral margin, corresponding to the zone occupied by the ciliary body. A ring of ossicles supports the eye, together with a sclera of hyaline cartilage. A plate of bone may surround the optic nerve. A nictitating membrane is present. The pecten, a plexus of blood vessels, projects into the vitreous body in the ventral half of the eye. Typically it is a folded membrane, highly vascular but with its blood supply independent of that of the chorioid. It is probably a nutritional device for the retina. Recently the bird pecten has had attributed to it the ability to perceive variations in magnetic intensities upon which the homing instincts of many birds depend. Direct evidence linking this body to the assigned function is lacking. The retina has great resolving power, due in part to the large size of the eye, the number of cones, and the "high ratio of optic nerve fibers to visual cells." Walls states that "the grand champion of all foveae (the depressed area in the

retina which is the region of greatest visual acuity) is perhaps that of the hawk (*Buteo*) in which Rochon-Duvigneaud found 1,000,000 cones per square mm. Even outside the fovea this hawk, with its approximately man-sized eye, has nearly twice the resolving power of human focal vision; and foveally, the visual acuity of some hawks and eagles reached a value at least eight times that of man."

The mammalian eye has already been described, but additional features may be noted here. There are differences among the Protheria, Metatheria, and Eutheria. In the first the eyes show many reptilian characteristics. In the Metatheria (marsupials) generally, the nocturnal type of eyes prevails, although among the kangaroos diurnal eyes occur. The placental mammals with such diverse representatives as moles, bats, seals, whales, and typical land forms show adaptations to these various habitats. To describe these individual changes is beyond the scope of this volume.

Nerve and Blood Supply to the Eye. The following description, based primarily on the dissection of the human eye, applies with some exceptions to the remaining mammals. Both sensory and motor nerves pass to the eye (Fig. 162). The motor nerves enter the eyeball by two long and about six short ciliary nerves. The long ciliary are branches of the nasociliary nerve, which in turn is a branch of the ophthalmic division of the fifth cranial nerve, the trigeminal. These long ciliary nerves contain sensory, parasympathetic, and sympathetic fibers; the latter are motor to the dilator pupillae muscle, and the parasympathetic are motor to the ciliaris and the sphincter pupillae muscles. The sympathetic nerves originate in the superior cervical ganglion and surround the internal carotid artery as the internal carotid plexus. Some of these fibers join the nasociliary nerve temporarily, leaving it to take part in the formation of the long ciliary nerve. The parasympathetic fibers are associated with the oculomotor nerve.

The small, reddish ciliary ganglion receives three roots, one sensory, from the nasociliary nerve; another motor, a branch of the oculomotor nerve; a third, a sympathetic twig from the carotid sympathetic plexus. From the ciliary ganglion six short ciliary nerves pass along the optic nerve and subdivide at the back of the eyeball into some 15 to 20 fibers before entering it.

The six muscles which attach to the eye and the levator palpebrae superioris, which retracts the upper lid, are supplied by three cranial motor nerves. The oculomotor nerve passes through the superior orbital fissure after dividing into two branches. The upper of these branches supplies the superior rectus and the levator palpebrae superioris muscles; the inferior ends in the medial and the inferior recti and the inferior

oblique muscles. The abducent nerve traverses the superior orbital fissure to the lateral rectus.

The trochlear nerve emerges by the superior orbital fissure at the level of origin of the lateral rectus muscle and enters the inferior rectus muscle. The orbicularis oculi muscle encircles the eyelids and is active in drawing the skin and eyelids medially, in blinking, and in closing the eye lightly. It receives motor branches from the facial nerve and sensory twigs from the trigeminal nerve.

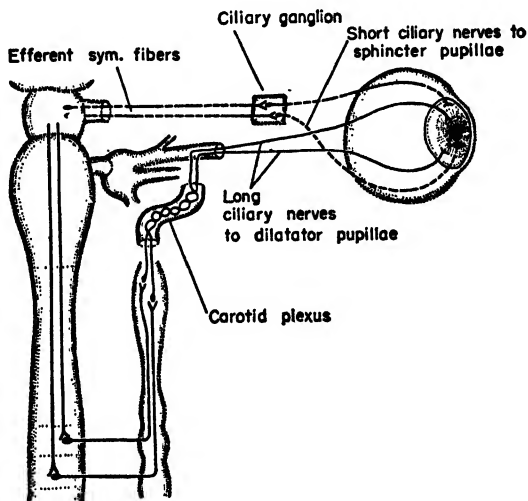


FIG. 162. Motor and sensory nerve supply to the eye. The pupil is dilated or constricted by appropriate nerve impulses, which traverse the nerves indicated. (After Gray.)

The eye is supplied by the ophthalmic artery, a branch of the internal carotid artery at the level of the optic chiasma in the floor of the mammalian brain case (Fig. 163A, B). The ophthalmic artery passes through the optic foramen and into the orbital cavity lateral to the optic nerve. Crossing over the nerve, it breaks up into ocular and orbital branches. The ocular twigs supply the eyeball and the eye muscles, while the orbital are distributed to the lacrimal gland and the facial region about the eyes. Venous drainage from the ocular area is through superior and inferior ophthalmic veins which open into the cavernous sinus in the floor of the brain case. The facial region about the eye is drained by the anterior facial vein.

Glands associated with the eye are the lacrimal, under the lateral

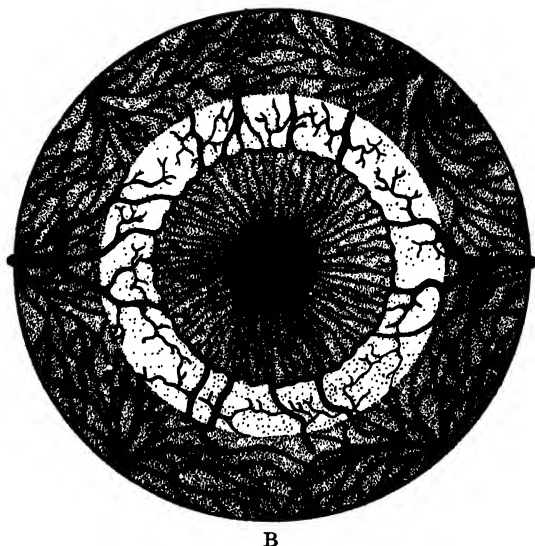
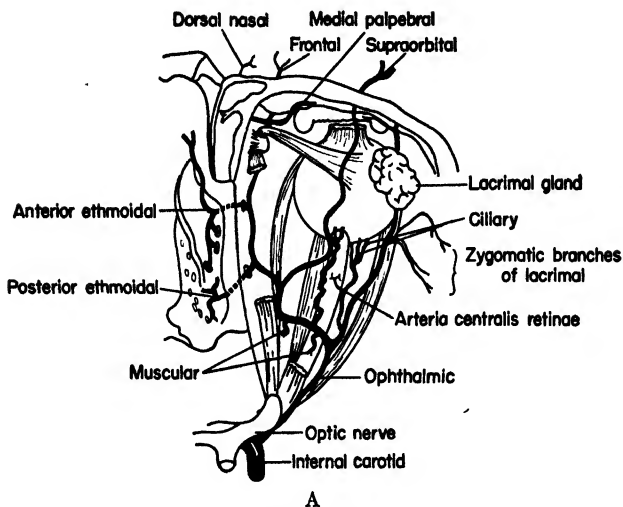


FIG. 163. *A* and *B*, blood supply to the eye. The ophthalmic artery offers the chief arterial blood supply. A small central retinal artery reaches the retina by coursing through the center of the optic nerve in the primates. *B*, cornea and iris are traversed by minute vessels. (After Gray.)

portion of the upper lid; the meibomian; and frequently the harderian. The lacrimal gland opens by a series of ducts in the upper lid. After bathing the orbit, excess fluid may be drained from the eye by the puncta lacrimalia, two small openings on the margins of the lids at the medial angle of the eye. The lacrimal ducts extend from these openings into a lacrimal sac and nasolacrimal duct and open into the inferior meatus of the nose. They have a germicidal, nourishing, and cleansing action. Tarsal, or meibomian, glands, elongate, finger-like sebaceous tufts, are found on the inner surface of the eyelids and open on the lid margins. They lubricate the eye and prevent overflow of tears. In animals with nictitating membranes, accessory lacrimal, or harderian, glands are commonly present at the inner margin of the eye and represent forerunners of lacrimal glands. This secretion is sebaceous and lubricates the eye.

The nictitating membrane, a third eyelid developed by a conjunctival fold at the inner corner of the eye, is transparent and permits moistening of the cornea without shutting out the light. It occurs in amphibians, reptiles, and birds. It is vestigial or absent in mammals.

The eye is moved nasally or laterally by the lateral and medial recti muscles and upward or downward by the superior and inferior recti and is rotated on its anteroposterior axis by the superior and inferior oblique muscles (Fig. 164). Movements within the eyeball by the sphincter and dilator pupillae constrict or dilate the iris, regulating the amount of light permitted to strike the retina, while the ciliaris muscle, of circular and meridional fibers, acts in accommodating the eye to objects within close range. It changes the convexity of the lens by acting on its suspensory ligament.

The eye opening is controlled by the orbicularis oculi, which closes the lids, and the levator palpebrae superioris, which retracts the upper lid.

The Ear. *Evolution and Development.* Among the invertebrates various balancing and orientation devices have evolved. Generally such mechanisms include either secreted or borrowed particles in close association with sensitive cells, the latter forming the lining of specialized sacs. Phylogenetically the chordate ear, too, is a balancing or static organ by which the animal is informed of changes in position. Originally it was a vesicle lined with sensory epithelium.

In the Acrania this organ is lacking, while in the Craniata there is a gradual evolution into a hearing organ from the lagena, an extension of the vesicle, which first appears in fishes. This structure culminates in the cochlea of birds and mammals. In the cyclostome lamprey, which has the most primitive vertebrate ear, it includes a single canal, which

may, however, represent a union of anterior and posterior canals; a utricle, and an endolymphatic duct directed to the surface. In *Petromyzon* an anterior and a posterior canal have separated from the vesicle and join the utricle at their ampullar and nonampullar ends. Sacculus and endolymphatic ducts occur. In the elasmobranchs, three well-defined *semicircular canals*, *sacculus*, *utricle*, and *endolymphatic ducts*, and a *lagna* have evolved together with sensory innervation (Fig. 165).

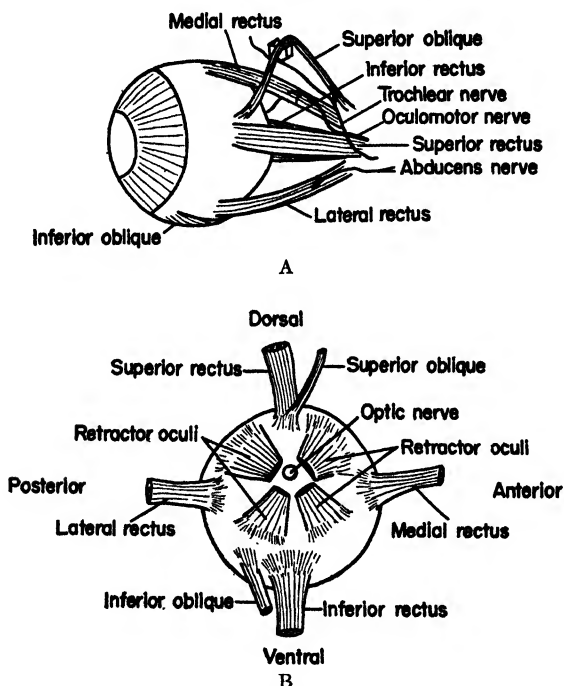


FIG. 164. Eye muscles. A, lateral view; B, posterior view.

The *lagna*, the first indication of a hearing organ, as noted, develops in conjunction with the static organ. The cartilaginous fishes do not rise above this level of ear development; the bony fishes, on the other hand, have evolved several features that convert the ear into a hearing organ. Further evolution of the hearing functions in higher vertebrates brings with it an external ear, an external auditory meatus, a tympanic membrane, ossicles, and a cochlea, not all of them developed in all vertebrate classes, as the following description will show.

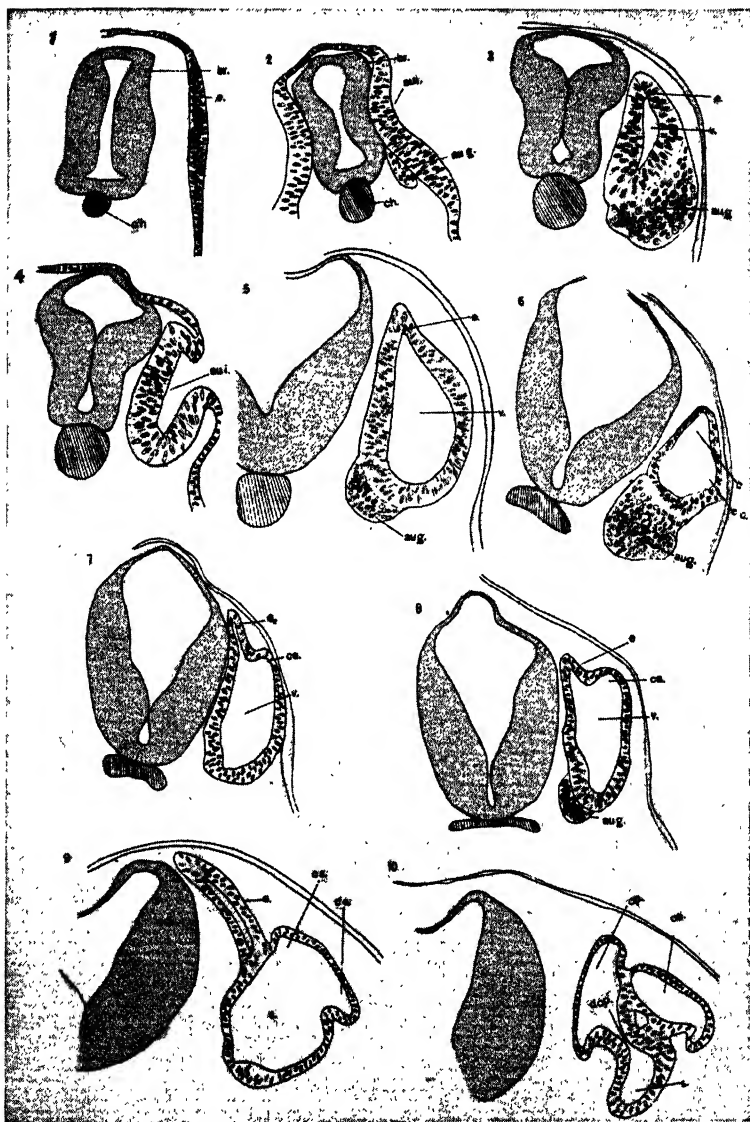


FIG. 165A. Development of the ear of the dogfish. Early stages, cross-sectional view.

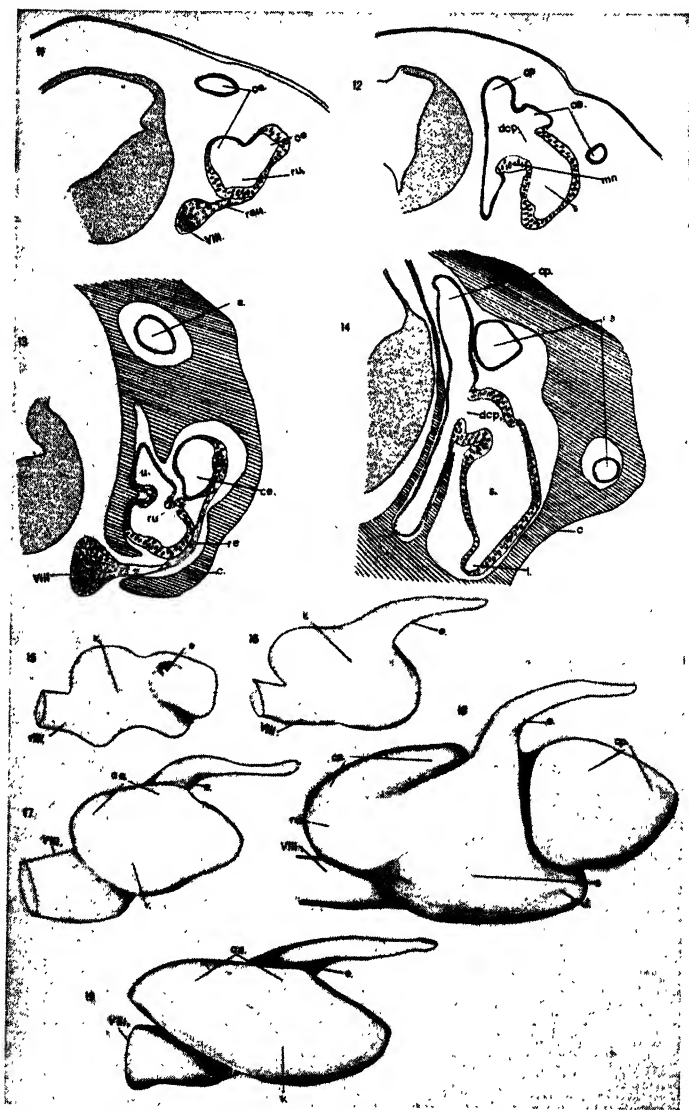


FIG. 165B. Development of the ear of the dogfish. Differentiation of the vesicles and semicircular canals.

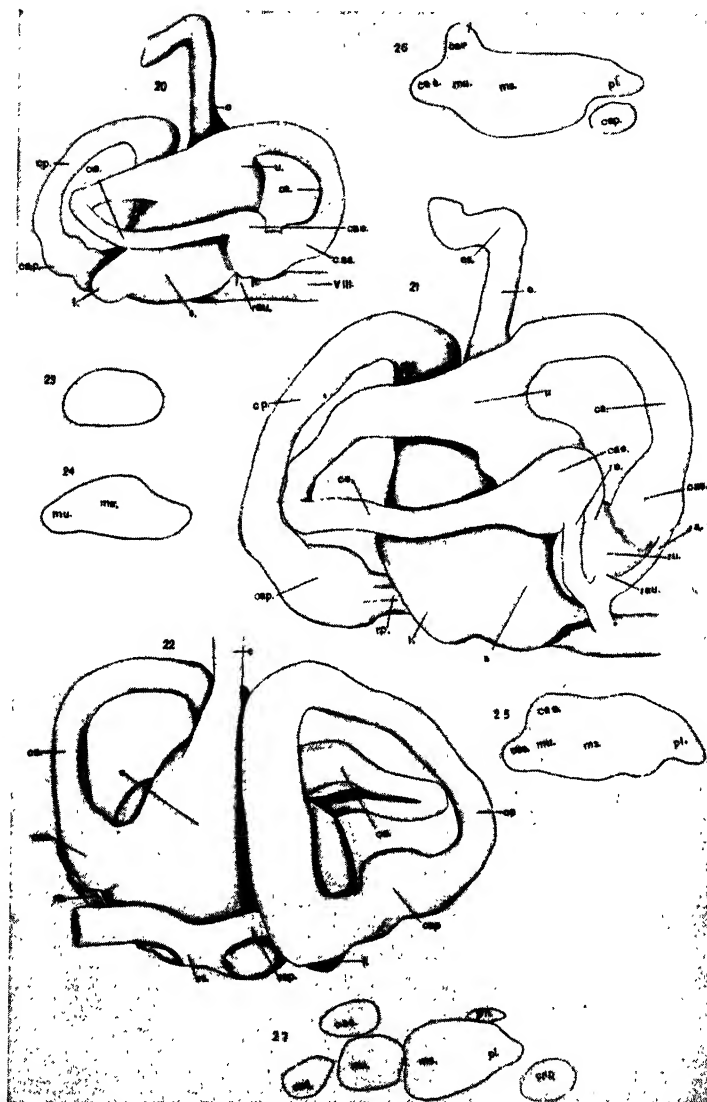


FIG. 165C. Development of the ear of the dogfish. The adult ear.

In the dogfish as well as in other vertebrates, the ear is a development of the lateral line system, more specifically from a pair of *lateral placodes*, one on each side of the dorsal midline in the epidermis at the level of the hindbrain. The first indications of auditory vesicles in *Squalus acanthias* appears in embryos of about 3.5 mm. before the closing of the neural folds. Concomitantly, the ganglion of the eighth cranial nerve descends from the region of the hindbrain to a position medial to the vesicle. The placode invaginates and forms a small sac, the *vesicle*. The latter communicates with the outside by the *endolymphatic duct*, whose pores may be perceived on the dorsal surface of the adult dogfish head on either side of the midline.

The *semicircular canals* are first recognized as outpocketings of the vesicle in the approximate positions they assume in the adult ear. Two canals lie in a vertical plane and one in the horizontal. As they become defined, a distinct enlargement, the *ampulla*, is formed in each canal, the anterior and lateral at the anterior end of the canals, where they join the vesicle; the posterior ampulla, on the medial side of the vesicle at the level of its floor.

The vesicle becomes further differentiated into a *recessus utriculus*, *utriculus*, *sacculus*, and *lagena*. Both ampullar and nonampullar ends of the anterior and lateral canals open into the utriculus, while the posterior canal forms a complete circle on the medial side of the sacculus and opens directly into this chamber. The recessus utriculus opens into the utriculus, and the latter, which lies dorsal to the sacculus, communicates with it by an elongate slit formed by a pair of internal limiting folds. Posteriorly the sacculus opens into the lagena. The three ampullae are partially lined with *ciliated sensory epithelium* raised into transverse ridges, one in each ampulla, called *cristae*. Ciliated sensory cells, arranged in patches, or *maculae*, are distributed also in various areas in the recessus utriculus, the sacculus, and the lagena; they are absent in the utriculus. The eighth cranial nerve divides into rami to supply the several parts. The *cochlear branch* of the auditory nerve to the lagena is a forerunner of the true nerve of hearing in higher vertebrates. *Otoliths*, small calcified particles, or sand grains occur commonly on the saccular floor. Movements of these particles in the endolymphatic fluid which fills the ear presumably make the animal aware of changes in its position by contacting sensory areas with varying intensities. Sensation in the ampullae is effected by movements of the endolymph against the raised sensory cristae which traverse them.

The human labyrinth is a balancing mechanism similar in many respects to that of the dogfish inner ear. In the dogfish the membranous

structures which include the semicircular canals and vesicle are surrounded by a cartilaginous brain case; the space between the canals and the case is filled with a fluid, the perilymph. In animals with bony skulls the same relations persist, except that a *bony labyrinth* surrounds the membranous. Only in the elasmobranchs does the endolymphatic canal open to the outside. The lagena evolves into the cochlear mechanism, which accepts and transforms sound waves into electrical disturbances affecting the brain centers. This we call hearing.

According to H. M. Evans, an English investigator, a hearing organ is developed in the carps (Cyprinoids), minnow, electric eel, herring, and other fishes. In the carp the swim bladder is attached to the vertebral column by a plate of bone, and extending from the anterior end of the bladder by a tube surrounded by a sphincter muscle under nervous con-

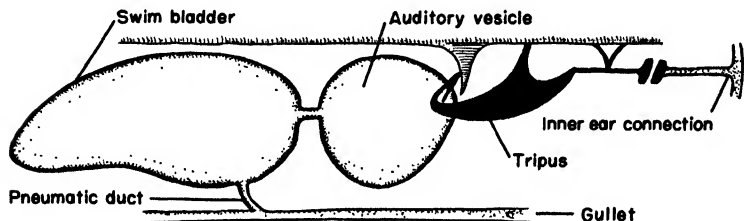


FIG. 166. Hearing mechanism in the fish. In the carp the swim bladder, a bony plate, a vesicle, and ossicles are joined to the inner ear and presumably transmit sound vibrations to it. (Redrawn from Evans.)

trol is an air vesicle (Fig. 166). This vesicle is connected with an ossicle by a muscle; the ossicle is one of a chain (weberian ossicles) uniting the vesicle with the inner ear. The swim bladder communicates with the gullet by a tube which permits swallowed air to enter the swim bladder. The mouth of this tube is surrounded with taste buds that permit air bubbles only to enter the bladder. The anterior vesicle is kept inflated to the proper degree for optimum reception of vibrations and acts apparently as a resonating chamber. External sound vibrations are transmitted through the body wall to this chamber and by way of the ossicles to the inner ear. Evans describes in the African elephant fish, *Mormyrus*, a hearing organ that includes a small window in the lateral skull wall covered by a thin osseous membrane, analogous to a tympanic membrane and a lagena in close association with the saccule. The lagena is the forerunner of the cochlea, the true hearing mechanism in higher vertebrates.

The Human Ear. The human ear is quite naturally separated into external, middle, and internal components (Fig. 167). The first includes the ear lobe, or auricle, the external auditory meatus, and the tympanic membrane; the middle ear extends from the tympanic membrane to the lateral wall of the inner ear. Within it are the three ossicles, malleus,

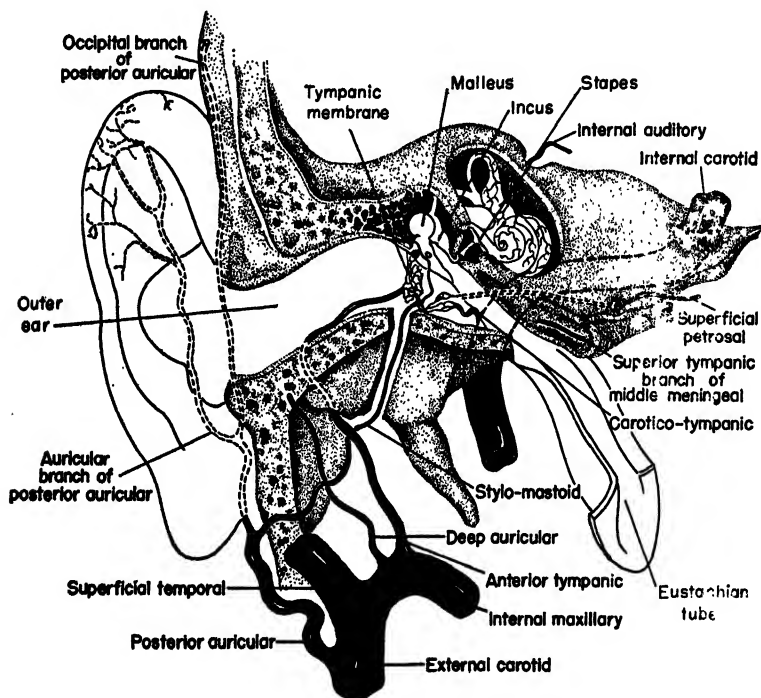


FIG. 167. The human ear. The outer ear extends from auricle to outer surface of the tympanic membrane. The middle ear is limited laterally by the tympanic membrane, medially by a bony wall. It contains the three ossicles and communicates with the pharynx by the eustachian tube. The inner ear contains the membranous and bony labyrinth and the cochlea.

incus, stapes; the inner ear includes sacculus, utriculus, three semicircular canals, and cochlea and is lodged in the petrous portion of the temporal bone.

The *auricle*, a sound-collecting device, except for its cutaneous covering, develops from mesenchyme at the margins of the hyomandibular cleft and is supported by cartilages. In the adult the parts of the auricle

have received distinctive names. In aquatic mammals like the seal, walrus, and whale, the auricle disappears. The *concha* is the communication of the auricle with the *external auditory meatus*; the latter, a canal extending medially in an S-shaped curve to the *tympanic membrane*, is lined with a thin layer of skin which also extends over the lateral surface of the tympanic membrane. The meatus, about an inch long in the adult, is derived from the first pharyngeal groove. *Ceruminous glands* in its walls secrete earwax.

The tympanic membrane, about 0.1 mm. thick, separates the outer from the middle ear. It has three layers, an outer cutaneous, a middle fibrous, and an inner mucous coat. On its inner side is attached the handle, or manubrium, of the *malleus*. The upper part of the membrane, the *pars flaccida*, is less tense than the lower and larger area surrounding the attachment of the malleus. The tympanic membrane transmits sound vibrations to the inner ear by way of the ossicles.

The middle ear, an irregular space within the temporal bone, also called the tympanum, includes a *tympanic recess* above the ear drum. In the latter recess the upper part of the *malleus* and the larger part of the *incus* are contained. Posteriorly, the cavity communicates with the *tympanic antrum* and, through it, with *mastoid air cells*. The antrum is a further air space above the mastoid air cells; the latter are irregular spaces in the substance of the mastoid bone. Passing anteriorly, the auditory canal (eustachian tube) unites the middle ear with the nasopharynx. The eustachian tube and the cavity of the middle ear are derived from the spiracle, prominent in the cartilaginous fishes. This, it will be recalled, was originally the cleft between the mandibular and the hyoid arches.

By the eustachian tube the pressure within the middle ear is maintained at atmospheric level. Sudden changes in external pressure require rapid adjustment of the pressure within the middle ear, as anyone who has made a quick airplane or elevator ascent or descent can verify. The tube is lined with a ciliated mucous membrane. This membrane lines the tympanum, antrum, and mastoid air cells and is reflected over the ossicles and the muscles. The ossicles in the middle ear, as indicated, transmit sound waves, striking the tympanic membrane, to the cochlea of the inner ear. The handle, or manubrium, of the malleus is directly joined to the tympanic membrane. To the manubrium also is attached the tensor tympani muscle, whose function may be read from its name. The head of the malleus in the epitympanic recess articulates with the body of the incus. The latter, which resembles a tooth with two roots, articulates with the *stapes* by the longer of the roots. The head joins

the stapes; the *stapedius muscle* is joined to the neck. This muscle on contraction increases the tension of the fluid in the inner ear, while the oval base fits into the fenestra vestibuli of the inner ear.

On the medial wall, opposite the tympanic membrane of the middle ear, are two windows, the *fenestra vestibuli* (ovalis) and *fenestra cochleae* (rotunda), leading into the internal ear. As indicated, the base of the stapes fits into the fenestra vestibuli; the fenestra cochleae leads into the cochlea.

The inner ear comprises a bony and a membranous labyrinth within the petrous portion of the temporal bone (Fig. 168). The *bony labyrinth*, differentiated into vestibule, cochlea, and semicircular canals, is hollowed from the bone. These bony channels, lined with periosteum, surround the membranous labyrinth. Between the bony shell and the membranous labyrinth is a space filled with a thin, clear fluid, the *perilymph*. In addition to the fenestra vestibuli and cochleae there are numerous smaller holes in the bony vestibule for the passage of nerve filaments and vessels to the membranous labyrinth. The bony vestibule houses the sacculus and the utriculus, while the cochlea extends anteriorly from the vestibule. It is a coiled bony tube of $2\frac{3}{4}$ turns about a central axis, the *modiolus*. In section it resembles a spiral staircase with gradually increasing spirals from top to bottom; the inner rail and circular wall are analogous to the modiolus. The modiolus has numerous perforations for transmission of nerve filaments from the cochlear nerve.

The *membranous labyrinth* follows the excavations in the bone, except for a division of the vestibule into sacculus and utriculus. The relations of the semicircular canals are similar to those in the dogfish, except that all three open by their ampullar and nonampullar ends into the utriculus. The membranous canals and the vestibule are filled with *endolymph*. The *endolymphatic duct* ends blindly on the medial side of the ear near the dura of the brain. Those parts of the internal ear concerned with balance are essentially similar to those of the dogfish ear. Sensitive *maculae* in the vestibule and *cristae* in the ampullae are stimulated by changes in position of the body. Two small crystalline bodies, the *otoconia*, are suspended in the endolymph in contact with the maculae. Upon stimulation the latter induce reflexive or willful actions and new bodily adjustments may follow, or awareness of the new position may occur without postural change.

Hearing becomes possible through the interaction of tympanic membrane, ossicles, cochlea, and central nervous system.

Inside the bony cochlea an osseous *spiral lamina* extends laterally

from the modiolus and partly divides the cochlear tube into an upper *scala vestibuli* and a lower *scala tympani*. In life a *basilar lamina* between the free edge of the spiral lamina and the outer wall of the cochlea completely separates the two scalae except at the top, or *cupola*, where an aperture, the *helicotrema*, unites the two. The *scala tympani* starts at

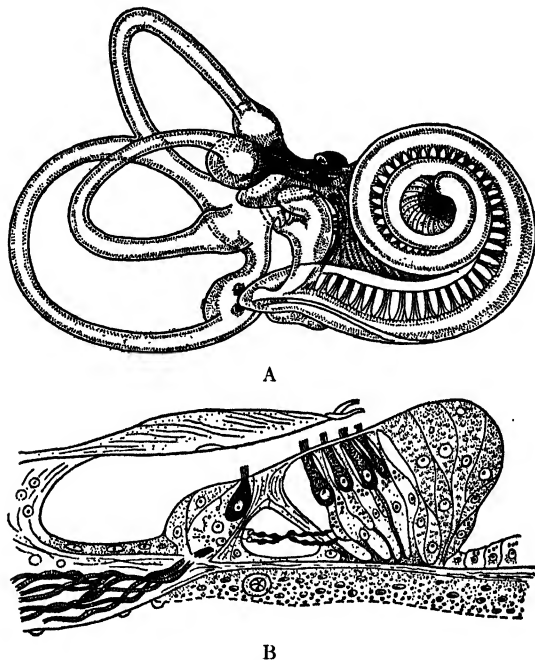


FIG. 168. *A*, the membranous labyrinth. The vestibular nerve supplies the semicircular canals, the sacculus, and utricle. The cochlear nerve is distributed to the cochlea. *B*, the organ of Corti. This structure within the ductus cochlearis receives sound impulses presumably by the hair cells, whence they are taken up by the cochlear nerve. (After Gray.)

the fenestra cochleae, which is covered by the secondary tympanic membrane; the *scala vestibuli* originates at the vestibule.

A third spiral, the cochlear duct, or *scala media*, is formed by a vestibular membrane stretching diagonally from the lateral wall of the *scala vestibuli* to the basilar membrane on its floor. Its lower end originates at the cochlear recess, an extension of the vestibule, and its upper end terminates at the cupola. It communicates with the sacculus by a

short *ductus reuniens*. On the floor of the scala media, and placed on the medial part of the basilar lamina, the spiral organ of Corti extends throughout the cochlear duct and represents a complicated epithelial structure, composed of (1) the inner and outer rods of Corti, inclined toward each other at their tips and enclosing the tunnel of Corti between them; (2) an inner and outer row of hair cells, respectively, on the margins of the inner and outer rods of Corti; (3) supporting cells of Deiters and Hensen; (4) a reticular membrane through which the free ends of the outer hair cells emerge; (5) a tectorial membrane, a delicate shelf overhanging the inner portion of the organ of Corti (Fig. 168B). The auditory nerve separates into vestibular and cochlear branches. The first, the nerve of equilibration, supplies the vestibule and the semicircular canals beyond its vestibular ganglion in the internal auditory meatus. In common with other sensory nerves, this ganglion lies outside the brain. The vestibular branches pass through the perforations of the bony vestibule to reach their destinations on the maculae of the vestibule and the cristae of the ampullae.

The cochlear nerve, the nerve of hearing, has its ganglion in the spiral canal of the modiolus. Filaments pass through the modiolus to the inner and outer hair cells of the spiral organ.

Sound waves are carried via the auricle and external auditory meatus to the tympanic membrane and set this into vibration with the same frequency as the incoming waves. These vibrations are transmitted through the ossicles to the fenestra vestibuli, whence they are carried to the scala vestibuli. At the apex of the cochlea the waves are carried through the helicotrema to the scala tympani. The scala vestibuli and scala tympani are filled with perilymph, and the vibrations affect the hair cells in the spiral organ, or scala media, and cause the sensation of hearing. The scala media is filled with endolymph and is continuous with the endolymphatic system of the semicircular canals, sacculus, and utricle. Presumably the basilar membrane stretching between the spiral lamina and the outer cochlear wall is the resonating apparatus, affecting the hair cells and translating the sound waves into the sensation of hearing. The sensations are transmitted to the auditory centers in the temporal lobes of the cerebrum.

It has been emphasized that the ear originally was a balancing organ. In the fishes the lagena, as noted, represents the forerunner of the cochlea. In the Anura a basilar outpocketing appears in the lagena with its own innervation. In the higher reptiles, the birds, and the monotremes, this basilar moiety develops into a curved extension which in the higher mammals evolves into the coiled cochlea. In all these groups above the

Anura its only connection with the sacculus is through a narrow channel, the ductus reuniens.

The middle ear, including the eustachian tube, first appears in the anuran Amphibia (Fig. 169). It is absent in the snakes among the reptiles. In some mammals, accessory air pockets are irregularly placed in the mastoid bones. In others, including many carnivores and some primates, extensive ventral pockets, the tympanic bullae, are formed.

An outer ear is lacking in Amphibia and in many reptiles, and the tympanic membrane may be observed directly on the surface of the head. In certain reptiles and in birds, a short external auditory meatus

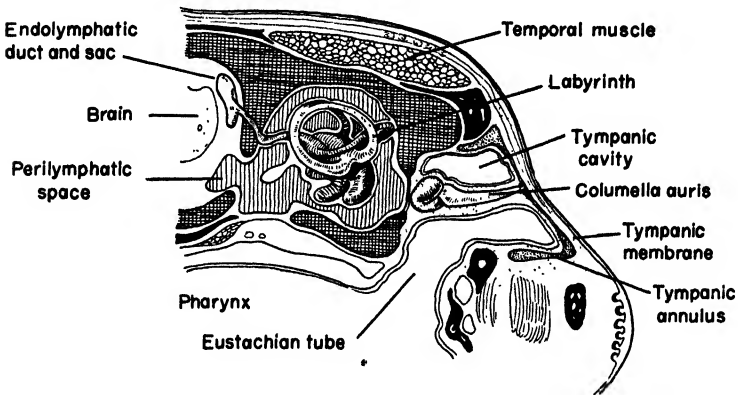


FIG. 169. Cross-sectional diagram of the right ear of the frog. Note the relations of the tympanic membrane to the surface and to the eustachian tube; the endolymphatic duct and sac terminating in the brain case and the relation of the columella auris to the perilymphatic space. (After Nierstrasz and Hirsh.)

leads to the membrane. Its external opening is usually guarded in these cases by small skin folds.

The ear bones are gill-arch derivatives, the stapes from the upper end of the hyomandibular, the malleus from the articular portion of Meckel's cartilage, and the incus from the quadrate portion of the palatoquadrate cartilage of the upper jaw. Their development and fate are considered in greater detail in the description of the skeleton.

SIDELIGHT

Vultures (*Pseudogyps africanus*) seemed scarce on the African plain. Now and then a tiny, moving dot, perhaps 7,000 to 10,000 ft. up, was pointed out to us as a soaring vulture and led to the remark that a flock of these scavengers soaring at 10,000 ft. altitude might police all of Africa. The visual acuity of

these great birds is unbelievable, perhaps eight times that of man. It was but a moment or two after the emperor of the jungle, a great 14,640-lb. elephant bull, was brought down that the vultures appeared. In an opening of the ominous forest, beside a dried stream bed where the great proboscidian fell, buttressed ironwood trees, towering over 135 ft. in the clean highland air, formed a magnificent avenue for the monarch. Looking up from our task of measuring the gargantuan body, we noticed perhaps a hundred first arrivals. As the moments passed, the branches became weighted with them. Becoming bolder, the late-comers approached more closely, like messengers of fate, giving by their mere presence silent warning of impending doom. A certain orderliness marked their descent. As the distant branches became crowded, those in the rear ranks passed over the nearer columns to take up new points of vantage. Silently and patiently they waited. Doubtless they observed our every incision, but without audible critical comment. The eye had led them to this spot. When night fell, they continued their wake. Now and then the flickering flame from the camp-fire was caught and reflected from a burnished breast or from the polished wing of one of these silent watchers.

Other visitors had become attracted to a possible feast, but through another sense organ, the nose. The bark of the jackal announced the presence of lions. Hyenas, emboldened by the night's darkness, slunk into the penumbra of the fire, our flashlights reflecting their hungry eyes. We counted 27 pairs, prowling and hoping, just as the vultures above were waiting and hoping. The nostrils promised a feast perhaps more appetizing to their possessors than the eyes foretold to the vultures.

The second day after the dissection we returned to the spot. Bare bones, some carried as far as half a mile, were the sole remains. In the meantime, myriads of enameled *Dermestes* beetles, also attracted through smell, had found the spot, as had flies, which in the interval dotted the flesh with eggs, now advanced to a squirming mass of maggots in the ripening tissues.

On the hunt our trail frequently crossed that of the rhinoceros. As we marched silently and in single file in the early morning through open forest, our senses became momentarily lulled by the endless beauty of the scene or by lack of sleep. We were hunting buffalo, and the rhinoceros was on the forbidden list. The unexpected, explosive snort of the rhino transported one instantly from the twentieth century to a remote time when life was tied very closely to the alertness of the senses. The eyesight of the rhino in shaded forest is probably poorer than that of man. To compensate, ear and nose appear doubly sensitive. In such an encounter the rhino probably does not see the hunter; he smells him. The animal paws the ground and may make a few of what the English call "swank charges," short, rapid advances. The hunter's senses, equally alert, bid him run; his judgment tells him to remain motionless. Sense matches sense. The eye of the human antagonist in this encounter tries to decipher the moves of the other, just as nostril and ear of the rhino test the air for the position of the enemy laden with threatening scents. Without reason, the great beast whirls sharply and crashes headlong through the forest.

Olfactory endings and tracts, mitral cells and thalamic centers in a formalin-preserved specimen do not carry drama when dissected. Countless hazards from which they have delivered the animal, rich feasts to which they have guided it, overwhelming sexual activities to which they attracted it, the constant tireless role they have played in its preservation—these are not mirrored in dead nerve tract or olfactory bulb. The dynamic nature of living stuff is forgotten or may never be imagined if the sole experience of the dissector is confined to such an examination of dead specimens.

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CHAPTER 8

THE DIGESTIVE SYSTEM

GENERAL CONSIDERATIONS

A superficial survey of the vertebrate digestive system might lead one to dismiss it rather hastily and lightly as a relatively simple affair. Its phylogeny as well as its individual development in embryonic life appears to be nothing more than a series of simple steps beginning with an invagination of the blastula to form the gastrula stage; a subsequent elongation of the enteric cavity so produced; a differentiation of this enteron into fore-, mid-, and hindgut, with the addition of mesodermal elements that surround the enteron of endodermal origin; the association of digestive glands with the elongate tube which traverses the body; and, concomitant with these changes the association of the nervous and vascular systems. A specialized part, the mouth, differentiated in close correlation with the pharynx, would appear to complete the picture.

This, as stated, might lead one to evaluate the system as simple in structure and in function. Analysis soon reveals how erroneous such a concept is. Functionally the system supplies the whole organism; it is a servant to the entire body and taken by itself has only academic interest or meaning. The sum of its activities, then, is correlated with those of the entire organism, and in this key position it is carefully conserved and guarded. Some of these safeguards, in the guise of tasting and smelling organs, either invite or warn against introduction of substances. These agents cannot protect the organism once harmful substances have entered the great digestive mill. In such cases, purging and vomiting represent the last-ditch defense of the tract against noxious or toxic introductions. The tract takes what is supplied after these offerings have once passed the guards at the gate. In these protective mechanisms, then, we already embark on the complexities of the system.

In connection with its functions the digestive system has called forth other modifications and surrounded itself with further safeguards. The smelling sense has already been mentioned; eye and ear also are called into play in the grim game of food getting. The visual acuity of the hawk very likely has developed in part in connection with its sighting of small living food in the guise of field mouse or dove. The olfactory sense

of fox, hyena, or lion is called upon constantly to locate food. Claw of lion, talon of eagle, constrictor muscles of boa are devices to subdue the potential meal. Poison fang of reptile, piercing points of barracuda, razor-edged placoid teeth of sharks, canine and carnassial tooth of carnivore, cropping incisor of ungulates, grinding molars of proboscids—all are necessary digestive adjuncts associated with levels of being, particular modes of life, and peculiar food habits.

Besides these very essential attributes of digestive systems, the digestive function itself requires the orderly working together of a number of internal aids, among which salivary glands, mucous glands, pancreas, liver, intestinal glands, bacterial flora, secretory and trophic nerves, nervous reflexes, and hormones should be mentioned. The essential function of a digestive system is to convert the food, which presents itself as carbohydrates, proteins, and fats, into solution, which also involves a breakdown of these foodstuffs into simpler and more easily absorbable combinations. When the food is in solution, it must be brought into close proximity with the blood supply so that the solutions may pass through semipermeable membranes and be transported either to food reservoirs or to various sites for immediate utilization. The mode of this food utilization and distribution is entirely outside willful control, *i.e.*, this regulation is automatic. But although automatic, it may be profoundly affected by conditions outside the tract. Speed of digestion is greatly affected by the nervous state of the body. Everyone has had the experience of a "digestive upset" as the result of emotional excitement during a meal. Today gastric ulcer is frequently attributed to the habitual overexcitement and punishment inflicted upon the nervous system by a mode of life that involves constant stimulation and excitation of the cerebral system.

To gain a clear insight into the components of the vertebrate digestive tract, let us review briefly the chief steps in its formation in the human being.

DEVELOPMENT OF DIGESTIVE TRACT

It will be observed in Fig. 170 that the *primitive endodermal gut* is laid down over the yolk and that it is covered by the splanchnic layer of the developing mesoderm. Together these two layers form the *splanchnopleure* and will eventually form the mesodermal and endodermal components of the digestive tract. With these changes, the lateral boundaries of the embryo become narrowed, resulting in an intraembryonic and an extraembryonic division of the gut, the latter represented by the yolk sac. *Fore-* and *hindgut* are first differentiated as rostral and

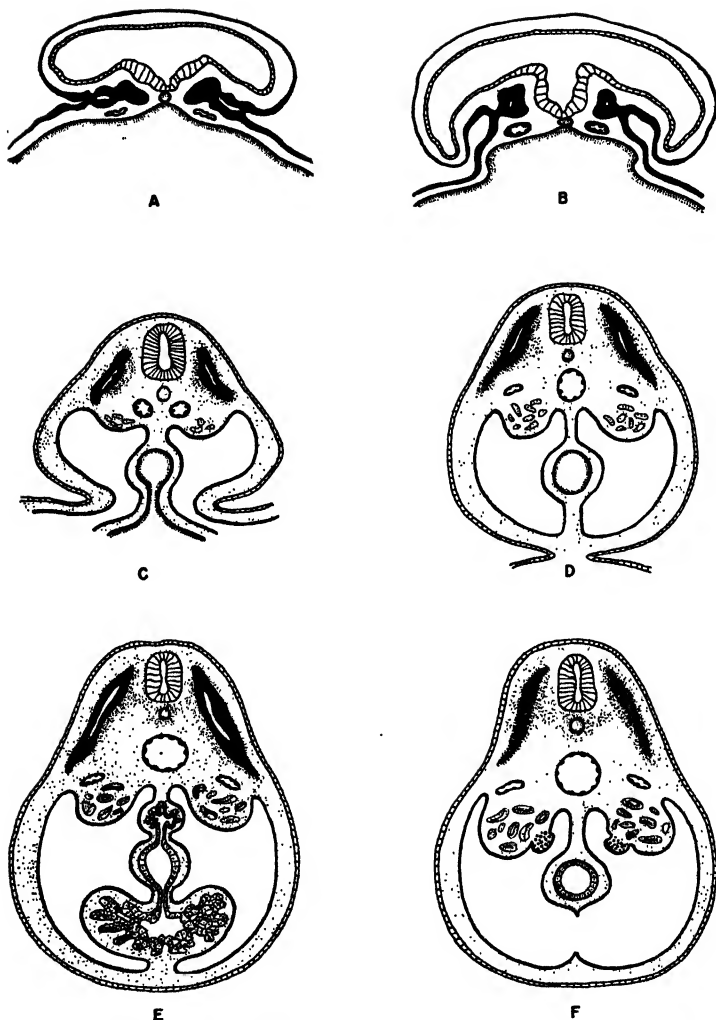


FIG. 170. Cross-sectional views of the developing intestine. A, the gut is first laid down over the yolk. B, with increasing utilization of the yolk, the definitive intestinal tract begins to constrict about the decreasing yolk mass. C, the somatic layers of the body wall separate from the splanchnic layers of the intestine. D, the celom is defined in the space between somatic and splanchnic mesodermal layers. E, with completion of the intestinal tube, secondary evaginations form the liver and pancreatic diverticula. F, the ventral mesentery largely disappears, leaving the intestine suspended by the dorsal mesentery.

caudal extensions of this developing tube, while at this stage the *midgut* remains in open communication with the yolk sac. Eventually the yolk stalk becomes constricted, and with these changes *mouth* and *anal openings* break through. Differentiated from the gut, even in early development, are several structures which later play a significant role in the body economy (Fig. 171). These include *Rathke's pouch*, an invagination from the stomodeum, and the *pharynx*, the latter a widened part of the gut caudal to the mouth opening; in mammals four pairs of pharyngeal pouches expand this latter division further but do not break through to the surface; at the level of the last pair of pharyngeal pouches

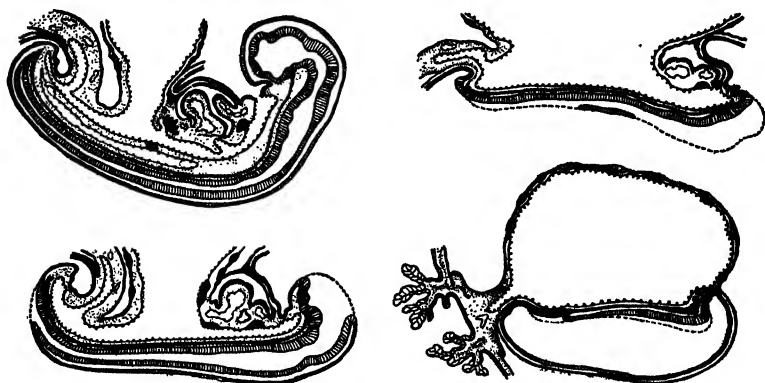


FIG. 171. Diverticula from the gut. Rathke's pouch, pharyngeal pouches, lung buds, liver, and pancreas represent outgrowths from various sections of the gut wall. (After Patten.)

the *lung buds* grow from the floor of the gut as ventral evaginations; this region is succeeded by a narrowed portion of the gut, the *esophagus*, which gives way caudally to a dilated section, the future *stomach*, *liver*, and *pancreas*, the liver a ventral diverticulum of the gut just caudad to the stomach, the pancreas from a dorsal bud at this level and a smaller ventral one associated with the liver. The intestine has begun its elongation at this stage of approximately 6 weeks in the human embryo and loops into the yolk sac; the future *large intestine* is represented by the posterior slip of this loop. The latter enters the *cloaca*, which is still present at this period. The latter also has the mesonephric duct opening into it.

Tooth ridges and *tongue primordium* should be included among the embryonic tissues that are destined for digestive functions. The former

are dermal derivatives and first appear in the second month of human development, from epithelial thickenings in the upper and lower jaws. The tongue originates as a pair of lateral thickenings over the mandibular and hyoid arches in the floor of the mouth at 5 to 6 weeks. *Parotid*, *submaxillary*, and *sublingual glands* are epithelial growths, the first from the cheek region and the latter on the floor of the mouth.

EVOLUTION OF THE DIGESTIVE TRACT

Included as part of the digestive tract are the mouth, the teeth, and the lips. It so happens that the mouth is also an entryway into the pharynx. There is a fundamental difference between the mouth of the jawless chordates and those with upper and lower jaws, although both types are similar in derivation. In the former it is represented by a cone-shaped cavity; the base of the cone is supplied with tentacles in *Amphioxus*, and the sides of the cone are studded with horn teeth in the cyclostomes. In the vertebrates with hinged lower jaws, the mouth embryonically is derived from the *stomodeum*. The foregut, it will be recalled, pushes rostrally and is met by a stomodeal depression from without the embryo. Approximation of foregut endoderm and stomodeal ectoderm results in an *oral plate*, and the rupture of this plate leaves a definitive mouth opening. In the gilled forms, the pharynx, with its lateral gill slits, is an interruption between mouth opening and esophagus; in the lung breathers the transition from mouth to esophagus is direct, and the lungs, as noted, grow from the foregut floor as a ventral diverticulum. In toothed forms there is another interruption between the mouth cavity and the lips. This results from the position of the dental ridges on the upper and lower jaws. Between their lateral margins and the inner margins of cheeks and lips, a space, the *vestibule* of the mouth, is formed. This is a sizable space in certain mammals and serves as a temporary food pouch in many rodents. Outwardly this space is limited by the *lips*, which are variable in their development. They are prominent in mammals, and, supported by a circular sheet of striated muscle derived from the platysmal sheet (sphincter colli), they may act as prehensile organs in picking up or engulfing food. In man they have become further transformed into accessory organs of speech. In their earliest appearance, they are skin folds without underlying muscles and without any great degree of movement or flexibility, although even in some of the fishes they develop into prehensile organs with underlying cartilaginous or fibrous supports.

Hard and Soft Palate. In the turtles and birds lips are absent, the beak takes over their prehensile functions, and at the same time the beak margins may effectively seal the mouth.

With the continued and perhaps increasing use of the mouth as a prehensile organ, the jaws, originally represented by palatoquadrate cartilages above and by Meckel's cartilages below, receive additional supports. These supports are of two types. The one, resulting in jaws of bone by addition of membrane bones derived from scales, from without, has already been considered. The other, made up of bony premaxillary, maxillary, and palatine shelves, appears within the mouth. In addition to the jaw support another function is acquired by the appearance of a hard palate.

This function is associated with the passage of air from the exterior to the lungs. In fishes this is not yet a problem, since water is taken into the mouth, and only in the lungfishes might such a function be of significance. In certain Dipnoi and in the Amphibia the first step is taken in this direction with the appearance of perforated nasal pits leading into the rostral end of the mouth cavity by choanae. In reptiles these choanae lead into a potential nasopharyngeal duct through cooperation of the tongue, *i.e.*, by pressing the tongue against the roof of the mouth the cleft between the palatine shelves is closed, and mouth and nasal passage are thus separated. The horizontal palatine extensions pushing medially actually approximate in the Crocodilia and Chelonia. This is not a simple step, for it involves horizontal extensions of premaxilla and maxilla and a shift in position from the vertical to the horizontal of the palatine and pterygoid elements of the original jaw apparatus. To this *hard palate* is added caudally membranous tissue, the *velum*, which extends the nasopharynx almost to the head of the larynx. This last is the soft palate. The birds do not advance as far as do the Crocodilia or the mammals in this respect, since the nasopharynx is incompletely separated from the mouth cavity because of failure of the maxillary, palatine, and pterygoid elements to join in a hard palate. In other words, a cleft palate is retained. The tongue separates the oral and nasopharyngeal cavities in the bird. In mammals, where it is greatly developed, the *soft palate* is movable and in swallowing is elevated, completely shutting off the nasopharynx from the mouth. It is covered with mucous membrane, and its free lower border medially may be extended into a palatine *uvula*. From the base of the uvula in the Primates the mucous membrane is arranged into paired folds on either side, called the *arches of the fauces*, supported by muscle fibers. Between the anterior, or glosso-palatine, arch and the posterior, or pharyngopalatine, arch on either side the *palatine tonsils* are housed. These are aggregates of lymphoid tissue, proliferating lymphocytes, active in combating bacterial invasions and infections. Additional lymphoid tissue surrounds the aperture between the mouth and pharynx, or faucial isthmus, and forms what has been

called a "defense ring." Together with the palatine tonsils this lymphoid tissue encircles the entire pharyngeal opening. In the Cetacea, separation between the food tube and the air tube is complete. The blowhole, for example, on the head of the great whales leads into an unbroken tube joined with the larynx. Mouth breathing in such animals would be impossible.

Teeth. Teeth are rightly considered a part of the digestive system. Although they have had an evolution apparently independent of the intestinal tract, this evolution has worked hand in hand with adaptive changes in other systems. As the basis for these correlated adaptive changes in digestive tract and dentition, the food habits are probably responsible, although we could say with equal right that a particular type of digestive apparatus and dentition made specific food habits possible. If we assume a species gradually subjected to changed food habits, we must assume that those which responded adaptively, presumably through mutational changes in intestine and dentition, survived; hence the correlated adaptations among systems which occur again and again in the animal kingdom. The result is that the type of dentition conforms with the type of the digestive tract. Specializations of dentition, in herbivorous or carnivorous animals, in other words, are correlated with the specializations in their alimentary systems. This is a common phenomenon in the animal body and appears so inevitable and even necessary that we give little thought to it. It is found, for example, in the evolution of limbs, where skeletal and muscle changes are accompanied by adaptive vascular and nerve changes; in the ear, where adaptive changes in the ossicles are accompanied by appropriate changes in muscles and vascular and nerve patterns; or in the correlated appearance of a sound-producing mechanism with a sound-perceiving apparatus in certain insects. To explain these helpful and useful changes in organ transformation, we are thrown back, as indicated, on mutations for their appearance and operation, and yet to depend upon this explanation is to make excessive demands on the mutation concept. We may designate them as coordinated evolution. Ultimately, of course, the evolution of any body part resolves itself into coordinated evolution in which many subordinate parts change, along with the structures and functions of the part as a whole.

Teeth, structurally, may be traced to placoid scales, and their position within the mouth cavity in turn stems from the invasion of epidermis and dermis into the mouth and pharynx (Fig. 172). On these foundations is built a tooth architecture that with succeeding vertebrate classes departs more and more widely from the original placoid pattern. There

is no superficial resemblance between elephant molar and the triangular, razor-like edge of the elasmobranch cutting tooth, and yet their component parts may be referred back to the same formative elements in both.

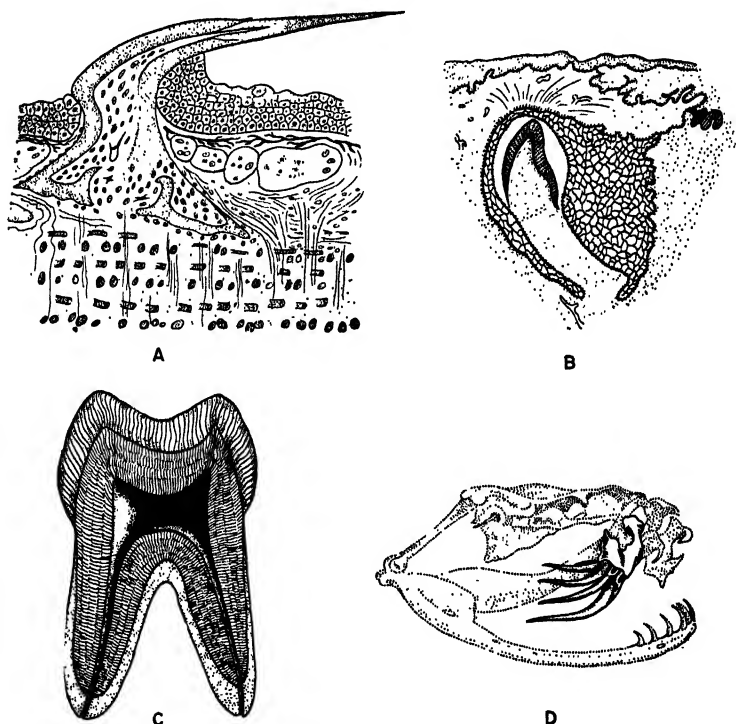


FIG. 172. Placoid scale and teeth. A, sagittal section through a placoid scale, showing base, pulp cavity, and spine; B, cross section through a developing tooth and dental ridge; C, vertical section through a molar tooth; D, the fang of the rattlesnake. The longest tooth in the upper jaw represents the functioning fang, others remain in reserve. Note the opening at the base by which the sac holding the venom opens into the hollow fang. With the opening of the jaw, the fang point is brought forward into the striking position.

Placoid Scale and Tooth. The placoid scale is derived from the *corium* as well as from the *epidermis* (Fig. 172). The corium lays down papillae whose outer odontoblast cells deposit a rectangular basal plate with a hollow center subsequently occupied by the pulp. The odontoblasts also

secrete the dentinal layer of the scale. The exposed surface, or spine, of the scale is a modified form of dentin, exceptionally hard and formerly believed to be enamel. While an enamel organ of ameloblast cells originally is present and overlies the developing dentinal layer, it is questionable whether it contributes to the formation of the placoid scale.

The tooth contains, as noted, a *pulp cavity* filled with *dental pulp*. The outer layer of the dental pulp is of *odontoblast* cells which during development secrete the *dentinal layer* to the outside of the cavity. The cells are extended into outer and inner processes; the outer, either by secretion or transformation, deposit uncalcified *pro dentin*, in which islets of calcification appear and convert the substance to *dentin*; the inner processes apparently regulate these activities. *Dental canaliculi* are formed in the dentin by the delicate odontoblast cell processes.

As the initial layer of dentin is completed, the cell recedes and deposits successive layers, which fuse with each other for the most part. Where fusion or blending does not occur, small interglobular spaces may be retained in the dentin. The dentin makes up the greatest part of the tooth; the term is synonymous with *ivory*. Two additional layers, the *enamel* and the *cement*, also constitute important structures of the tooth. Enamel, the hardest substance in the body, is secreted over the crown of the tooth. It consists of 96.5 per cent of mineral and 3.5 per cent of organic matter. Sodium phosphate, traces of magnesium phosphate, calcium carbonate, and fluoride are its chief mineral components. Enamel is laid down by the enamel organ of *ameloblast cells*, of epidermal derivation and is deposited in layers as a keratin-like substance from the ameloblast cells. These deposits then calcify to form the true enamel. With the secretion of successive layers, the ameloblasts recede, and with completion of this hard prismatic layer the cells apparently conclude their activities by elaboration of a dental cuticle. It must be remembered that the ameloblasts act from without, while the odontoblasts are secreting dentin from within. *Osteoblasts* surrounding the dental sac in which the root of the tooth is formed invade the region and furnish the cement, which is typically bone-like in structure and which constitutes the outer layer of the root.

The pulp cavity, filled with pulp, is the source of vascular nourishment and innervation for the teeth.

In the human embryo of 8 weeks, epithelial cell clusters appear on upper and lower jaws just inside the developing lips, to form dental ledges. Further epithelial clusters, budded from the dental ledges, form the enamel organs. These enamel organs assume goblet shapes within which the dental papillae of dermal origin proliferate; these papillae are the forerunners of the dental pulp. From the outer border of the

papilla, odontoblast cells secrete the dentin, while the ameloblast cells of the enamel organs lay down the enamel. The pulp becomes infiltrated with blood vessels and nerves.

Teeth in Vertebrate Classes. Elasmobranch teeth are quite generally flattened and triangular in shape (Fig. 173A). Their free edges are frequently serrated and may present several points, or cusps. In *Mustelus* the teeth are worn down and without points. One of the most striking features of elasmobranch teeth is their indefinite succession. A lower jaw of the shark, when cleared of its connective and membranous tissues, reveals on the lingual side several rows of teeth, beginning with the oldest row on the arc of the jaw and receding row upon row to younger generations of teeth. Such an indefinite succession is termed *polyphodont*. Already teeth at the piscian level show some degree of differentiation in various species, so that grasping as well as grinding teeth may be distinguished. This is known as *heterodont* dentition. The first teeth are without deep roots; they may be seated upon, or straddle, the cartilaginous or bony jaw. This mode of attachment is known as *acrodont* and usually accompanies the polyphodont condition.

The bony fishes exhibit greater variation in dentition than do elasmobranchs. They range in shape from the curved, needle-like piercing teeth of barracuda and moray eels to the flattened dental plates of the lungfishes. They are further distinguished by their distribution in the mouth and pharynx. Thus vomerine, hyoidean, and branchial teeth, arranged in small clusters, are present, in addition to those on the usual dentary and premaxillary sites. Apparently the additional teeth serve as holdfasts either for living prey or for relatively large pieces of food.

This same feature of wide variation in dentition characterizes many Amphibia. In some *Anura* (*Bufo*, *Ripa*), however, the teeth are completely absent. In the Amphibia, as traditional forms between water and land life, we should expect variations in dentition, just as we find them in other systems. If, for example, we compare the Amphibia with the fishes, we should conclude that the Pisces, on the basis of distribution, variations into aggressive species, and development of a wide range of characters which combine to make them masters of the sea and the fresh waters, are far ahead of the Amphibia. The latter, from one point of view, might be regarded as misfits; they could not compete in the water, and they have not advanced far on land. From another standpoint, however, they represent the restless geniuses who dared and, by daring, discovered an entirely new world, a new field of action for the vertebrates, the world of land and of oxygen in a twentyfold measure over that with which their piscian cousins contented themselves.

Their dentition arises either directly under the mucous membrane of



FIG. 173A. Photograph of a shark jaw, showing several reserve tooth generations. Tooth succession in the sharks is indefinite.



FIG. 173B, Jaws of sperm whale; the teeth are cone-shaped.



FIG. 173C, Detail of "whalebone" in a humpback whale (Mysticeti). The whalebone forms a fringe-like sieve attached to the upper jaws. View was taken from the dorsal surface.

the mouth cavity, to which a dental ledge is added underneath (urodeles), or their primordia may appear upon the dental ledge after this last structure is laid down (Anura). Polyphyodont succession is assured by younger tooth generations upon the dental ledges. The ledge must be visualized as a horizontal shelf extending lingually from the medial edges of the jaws. The functioning teeth are attached to the medial sides of the jaws and are therefore pleurodont from the standpoint of attachment.

In contrast to the large number of teeth, which may be in excess of 100 in some of the elasmobranch fishes, the number is reduced in Amphibia. The typical anuran and urodele tooth is cone-shaped, with two points, usually recurved toward the mouth cavity. The teeth on the vomer and palatine bones, in contrast, have single tines. In the common frog they are reduced to the upper jaw and the vomer bones. The larvae of Anura have horny plates which later are replaced by true teeth.

Most curious, and foreshadowing the teeth of some of the mammals, are the teeth of the fossil labyrinthodont Amphibia of the Triassic. Extreme folding of the dentinal layer, together with fusion of adjacent layers, separated in part by extensions of the central pulp cavity, produced a tooth singularly like the *selenodont* mammalian tooth. It is designated as *labyrinthodont*.

Reptiles. Wiedersheim and others have called attention to the three modes of attachment of reptilian teeth. They may be *pleurodont*, i.e., attached to the medial walls of the jaws; *acrodont*, i.e., seated on the ridges of the jaws; or *thecodont*, i.e., seated in alveolar sockets as in the mammals. All three types are represented in the Reptilia. The first type is represented by the dentition of many Lacertilia, chameleons, skinks; the second occurs in *Lacerta* and *Anguis fragilis*; the third is present in crocodiles and most fossil reptiles. The embryos of lizards, turtles, and some snakes develop an egg tooth at the tip of the snout which breaks the eggshell at hatching. Owen called attention to the close similarity of dental pattern in the Theriodontia, a giant group of fossil saurians from South Africa, and present-day carnivores. Incisors, canines, and molars were differentiated. Galeosaurus carried six incisors, paired canines, and a large number of molars. Other differentiations in fossil reptiles range from insectivore-like and herbivore patterns to a complete absence of teeth.

The general nature of snake teeth does not differ markedly from that of other reptilian orders, save for the development of poison fangs (Fig. 172D). In the dental pattern of the nonpoisonous European snake *Tropidonotus natrix* the teeth are arranged in four parallel rows that may number approximately 520. The pulp cavities in these snakes communicate with the marrow cavities of the jawbones.

In the poisonous snake *Vipera animodytes*, Leydig found 15 poison fangs on each side, arranged in rows, most of them reserve teeth. In other species only 9 occurred on each side. The first, or oldest, tooth is the only one articulating with the jawbone. Besides the pulp cavity a groove, or canal, on the lingual side of the tooth forms a channel for the extrusion of venom. At the base of the tooth an opening places the tooth in communication with the poison gland, a modified labial gland, while near the point of the fang a slit permits extrusion and injection of the poison.

The Gila monster, *Heloderma suspectum*, is provided with poison glands associated with the teeth, but hypodermic fangs do not occur.

In the Chelonia, teeth appear only transitorily in the embryonic stage, since they are replaced by horny beaks in the adults. This same condition applies to modern birds, but not to fossil genera like *Archaeopteryx hesperornis*, or *Ichthyornis*, the latter from the Permian beds of Kansas. These ancient types possessed teeth showing similarities with their reptilian forebears.

Mammals. The characteristics of the mammalian tooth and its development have already been described. There remains the problem of examining some of the differences and the specializations in mammalian dentition. One conclusion may be reached even before we examine the dentition in a few of the mammalian orders, namely, that the dentition has been highly adaptive and that peculiar development or overemphasis of certain teeth is correlated with specific methods of obtaining food. The highly adaptive feature of this dentition is perhaps its outstanding feature. From an original homodont pattern have evolved incisors, or cutting teeth, canines, or stabbing teeth, premolars and molars, and macerating, or grinding, teeth. Occasionally we meet such curious modifications as the single elongate lance of the narwhal or the tusks of the elephant, derivatives of incisor teeth, or even an absence or a great reduction in dentition, as in the Edentata.

In the Edentata the teeth are entirely absent in *Myrmecophaga* and *Mantis*, the spiny anteater. The whalebone or baleen whales (*Mysticeti*) are without teeth; the toothed whales (*Odontoceti*) have retained cone-shaped undifferentiated ones (Fig. 173*B* and *C*).

The marsupials, on the other hand, have the largest number of teeth among the mammals. In the opossum there are 50. From these high numbers there is a variable reduction, beginning with the last molar, in the true mammals. Besides this reduction is the well-known absence of upper incisors in the artiodactyls and the vestigial canines in the perissodactyls. In the rodents the incisors undergo a relatively great development with which is associated their continual growth during adult life.

The mammalian tooth distribution and differentiation are best expressed by dental formulas which at a glance indicate the types and their numbers in upper and lower jaw. Thus, the pig dentition in one-half of upper and lower jaw may be expressed as follows:

$$\frac{3}{3} I, \frac{1}{1} C, \frac{4}{4} PM, \frac{3}{3} M$$

This is commonly reduced still further to read

$$\frac{3 \cdot 1 \cdot 4 \cdot 3}{3 \cdot 1 \cdot 4 \cdot 3}$$

By doubling these values, the total number of 44 teeth in the pig are accounted for.

The human dental formula is

$$\frac{2 \cdot 1 \cdot 2 \cdot 3}{2 \cdot 1 \cdot 2 \cdot 3}$$

Certain sexual differences may appear, particularly in the canine teeth. The great tusks of the boar fail to develop if the male is castrated early in life; the male hippopotamus has larger tusks than the female. Aristotle, and later Cuvier, pointed out that if horns are present in an animal the canines are not developed.

Wiedersheim correlates the great differentiation of mammalian teeth with the appearance of the pterygoid chewing muscles associated with the lower jaws. In fishes, amphibians, and reptiles, the lower jaw movement is up and down. With development of the pterygoid muscles, lateral grinding movements were introduced which changed the nature of the mandibular articulation and may have affected the original homodont nature of the dentition. It should be remembered, however, that many mammals, particularly carnivores and certain primates, are incapable of any extensive lateral grinding movements, although they possess well-developed pterygoid muscles.

Characteristic, particularly of primate dentition, are the cusps, or tubercles, on molars and premolars, resulting in typical *bunodont teeth*. This type of dentition also appears in the pig. The grinding functions of ruminant teeth are possible because of the folded lamina of enamel between which the dentinal layers wear down more rapidly, resulting in a *selenodont* pattern. A modification of this pattern in the great fused molars of the elephant, with transverse ridges of enamel, gives rise to the "washboard-like" pattern known as *lophodont*.

Three theories have been advanced to explain the multituberculate

nature of mammalian teeth. These are the differentiation theory of Cope and Osborn, the concrescence theory of Röse, and a concentration theory of Bolk. The differentiation theory assumes the derivation of multituberculate mammalian teeth from the single cone-shaped haplodont teeth of reptiles (Fig. 174). By differentiation of an additional anterior and posterior cone, a three-pointed tooth would result. This condition is actually approached in *Dromatherium*, a fossil Triassic mammal, where these points are arranged in a straight line and the tooth has a wall, the cingulum, surrounding the base of the crown. By increase in size and realignment of the cusps, a triangular arrangement of the points might occur. Since the cusps of upper and lower molars do not meet point to point, it would be necessary for the anterior and posterior points in the lower jaw to move opposite to those in the upper. Cope and Osborn called the original cusp *protoconus*, the anterior *paraconus*, and the posterior point *metaconus*. Apparently, however, the *paraconus* and not the *protoconus* is the oldest cusp. In the lower molars *concooid* is substituted for *conus*. By differentiation of further points, a *hypoconus* and a *proto-* and *metaconulus*, a six-cusped tooth results. Paleontology and embryology do not support many of the details presented by this theory.

The concrescence theory holds, just as does the differentiation theory, that the haplodont reptilian tooth is the basis for the multituberculate mammalian tooth. Instead of resulting from differentiation of points, however, the molars are assumed to have arisen from the serial fusion of haplodont teeth as well as from fusion of adjacent tooth primordia. Ihle points out that such fusions actually occur in some mammalian teeth, although this is denied by some observers; further, Kükenthal believes that triconodont and multituberculate teeth may be explained by the concrescence theory, at the same time not denying the role of differentiation of single cone-shaped teeth.

The point of departure of the concentration theory of Bolk is that two tooth generations appear in close succession from the tooth matrix. These become joined so that the mammalian tooth represents a fusion of two elements. The theory leans in part on the fact that two rows of dental matrices occur in mammalian tooth development, the one responsible for deciduous, the other for permanent dentition. Bolk derives the six-cusped condition from the fusion of two triconodont teeth as they occur in the reptiles.

Besides variation in the number of teeth functioning at a given time in different classes or in species within a class of animals, there is variation in the succession of teeth. The *polyphyodont* condition represents an in-

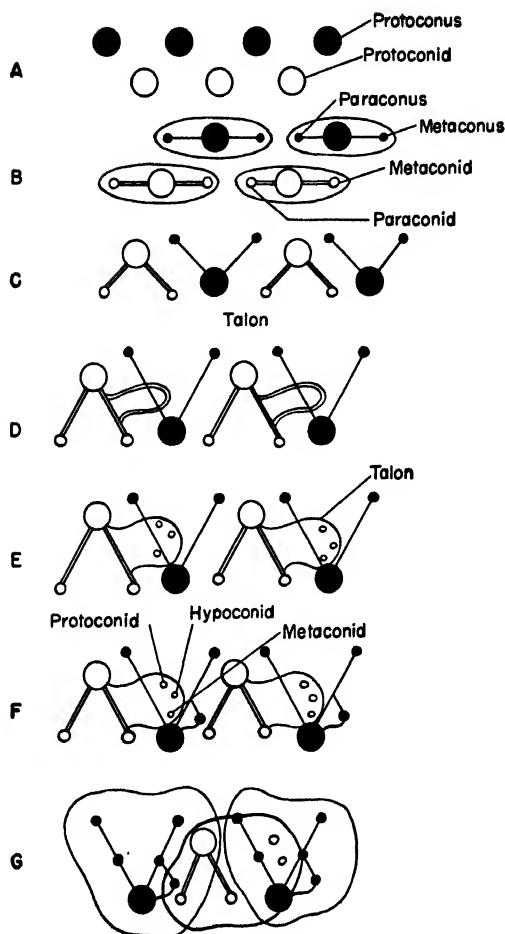


FIG. 174. To illustrate the Cope-Osborn differentiation theory of multituberculate tooth development. (Upper teeth in black, lower ones blank.) A, the original tooth is assumed to be cone-shaped. B, anterior and posterior cones differentiated from original cusp. C, realignment of the cusps results in their triangular arrangement. Note that upper and lower points move in opposite directions. D, a lateral outgrowth, the talon, provides the base for additional cusps. E, F, G, development of molar dentition by addition of talons on the posterior borders and additional cusps. E, fully developed molar tooth with as many as six cusps. (Redrawn from Ihle.)

definite succession and probably indicates the original state. This is reduced to the *diphyodont*, where deciduous teeth are followed by permanent dentition in mammals. This may be still further reduced to the *monophyodont* state. The latter may involve retention of the deciduous teeth in adult life or the loss of the primary dentition *in utero* as in certain rodents. Finally the *edentate* condition may mean an almost complete loss of teeth, as in the armadillo and spiny anteater, or a replacement of teeth by sharp beaks, as in the turtles and the birds. Additional terms are used to designate the specialized teeth of various mammals. Thus we find that *secodont*, or pointed, teeth are characteristic of Carnivora; *bunodont*, or blunted, cone-shaped cusped teeth characterize primates; *lophodont*, with enamel ridges on the grinding surfaces, characterize ungulates. The last may develop into *selenodont* teeth (washboard). These result from fusion and extension and joining of the enamel-tipped cusps. The proboscidian tooth is derived from the fusion of a number of dental laminae covered with enamel; cement joins the laminae.

The lips and teeth represent the gateway to the mouth. Both structures are much more than passive agents, however, particularly in the mammals, where the lips may evolve into prehensile organs and where the teeth become variously adapted, serving in the capture, maceration, or grinding of the food.

Tongue. With the gradual appearance of these highly significant structures occurs an evolution of the tongue and salivary glands (Fig. 175). The type of tongue, characteristic of vertebrates above the cyclostomes, begins as a slightly folded area of mucous membrane in the floor of the mouth of fishes. The fold overlies the basal segments of the hyoid arch, the basihyal cartilages. It is without its own musculature. This organ, the *primary tongue*, has added to it, beginning in the Amphibia and retained in the remaining classes above the fishes, a secondary *glandular tongue*, which becomes completely fused with the first. Some of the bony fishes bear teeth on the tongue, but glands and muscles are absent. In the Amphibia hypobranchial muscles migrate into the tissue underlying the mucosal lining. This musculature differentiates into protractor, retractor, and manipulative slips and may reach exaggerated proportions in the Anura and the chameleons. By its anterior attachment this secondary muscular tongue may be flipped out some distance from the mouth, and with the aid of secretions from its glandular components it becomes a useful tool in capturing insects (Fig. 176). In those amphibians which retain gills, fish-like bodies, and aquatic habits, the tongue shows a lack of muscular and glandular development and may be entirely absent, *e.g.*, Aglossa. With the rise of the secondary tongue in

land amphibians the glandular field on its original posterior margin joins the anterior margin of the primary tongue. The midpoint of this junction marks the original opening of the thyroglossal duct, indicated by a depression at the posterior terminus of a median sulcus on the dorsum of the tongue, the foramen caecum. The *thyroglossal duct* originally connects the thyroid gland with the mouth. The *median sulcus* is the slight groove left in the longitudinal midline of the tongue as the result of the development of the muscular portion. The latter arises from a ridge on either side anterior to the primary tongue. Growth and eventual fusion of the two muscular elements form the definitive tongue. The *hyoid arch* retains its tongue-supporting function throughout the vertebrate

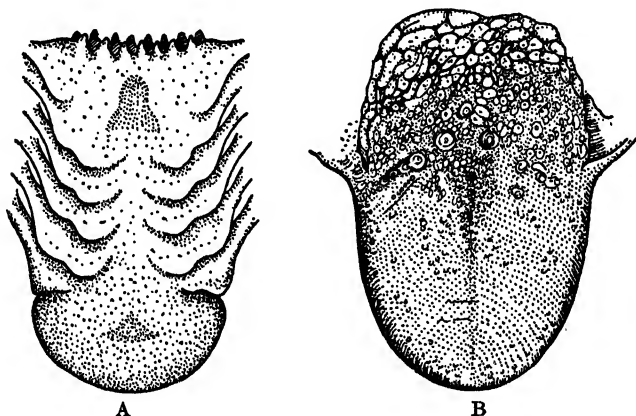


FIG. 175. A, elasmobranch tongue; B, human tongue. The elasmobranch tongue is a slight mucous membrane fold covering the hyoid arch. The human tongue is a muscular organ covered with a secreting mucous membrane, well supplied with taste buds.

series, articulating with the skull by a bony element at the styloid processes of the mastoid bone in the ungulates and by a ligament in others, *e.g.*, the primates. In the birds, instead of articulating directly with the skulls, the free ends of the hyoid processes may circle around the occipital portion of the skull and terminate subcutaneously.

The tongue of the birds is narrowed anteriorly in conformity with the shape of the lower beak. It is covered with a keratinized epithelium which may be raised into papillae or spines. In the parrots and ravens, as well as in some of the smaller carinate songsters, it is quite protrusible and muscular, and its flexibility makes possible the articulation of sounds imitative of those produced by other birds or of the human voice.

In the mammals the tongue is composite, as in other amniotes, and serves originally, through its extensive musculature, as a suctorial and exploratory organ. Later it becomes an effective mechanism in the manipulation and swallowing of food and in articulation. A further characteristic of the prosimian tongue is the development of a *sublingua*



FIG. 176. The chameleon tongue. When the mouth is closed, the tongue folds back upon itself. (This is an example of the possibilities inherent in animal photography. In this instance the chameleon took its own picture by completing a low-voltage electric circuit when its tongue touched the insect on the copper plate thereby discharging a flash lamp.)

under the muscular portion. This may be supported by cartilage and a fat pad but is without muscles.

The mucous membrane is well supplied with papillae carrying taste buds of various types (see *sensory organs*). In land animals these taste organs act as informative agents for determining the nature of the food.

Genioglossus and hyoglossus are paired muscles which connect the tongue with the hyoid bone; the root is further associated with the pharynx by the superior pharyngeal constrictor muscles and by mucous

membrane and with the soft palate by the glossopalatine arches. The styloglossus and the glossopalatinus represent the remaining extrinsic muscles. These four are particularly active in protracting and retracting the tongue. Four pairs of intrinsic muscles change the shape of the tongue in speech and in swallowing. Sensory nerve fibers are supplied by the fifth, seventh, ninth, and tenth cranial nerves, while the motor fibers to the muscles of the tongue are branches of the twelfth, the hypoglossal nerve. The chief blood supply is from the lingual and external maxillary branches of the external carotid artery.

ESOPHAGUS, STOMACH, INTESTINE

The intestinal tract is a tube of dual origin; the lining, including the associated glands, is derived from endoderm; the muscular wall, including the outer serous coat, is a development from the mesoderm (Fig. 170). Associated parts of the functional mechanism are blood and lymphatic vessels and nerves. The structure of the tube may be best understood in the light of its twofold function. Food is broken down and placed in solution through glandular activity by the mucosal lining and its glands, although these processes do not take place in the esophagus. Physical support for the food masses as well as their propulsion through the tract is assured by the muscular walls and associated mesenteries.

Histology of Esophagus. Before considering the changes in the tube from class to class, we shall examine briefly its histological character in the mammal (Fig. 177). Beginning at the outer margin, a loose connective-tissue layer, the *tunica adventitia*, attaches the esophagus to the various surrounding structures. It will be recalled that in mammals the esophagus traverses the entire thoracic cavity, and in its descent it lies, first dorsal to the trachea, then in close proximity to the lungs, heart, and thoracic aorta. Immediately underneath the *tunica adventitia* is the *muscularis externa* layer, composed of longitudinal fibers external to circular ones. Approximately the upper third of this layer is striated muscle tissue; the lower two-thirds is smooth muscle. The thickness of the muscular layer varies from $\frac{1}{2}$ to $2\frac{1}{2}$ mm. in moderately sized mammals. Inside the muscular layer is a *submucosa* of collagenous connective tissue and elastic fibers arranged in a network. A thin layer of smooth muscle, the *muscularis mucosae*, marks the division between submucosa and mucosal layer. The latter constitutes the inner lining of the esophagus and is of stratified, squamous epithelial cells. The lining, a continuation of the pharyngeal lining, is quite distinct from the columnar epithelial mucosa of the stomach. Glands in the esophagus are limited to a *mucous type* in the submucosa and *cardiac glands* in the

mucosa. The cardiac are scattered in the upper end of the esophagus and near the junction with the stomach. The mucous glands have a lubricating function; that of the latter is unknown. The blood supply to the esophagus is from *cervical*, *thoracic*, and *abdominal arteries*. The nerve supply is *sympathetic* and *parasympathetic* and is arranged in two plexuses, one the *myenteric* (Auerbach's) between the longitudinal and circular muscle layers, the other the *submucosal* (Meissner's) inside the circular muscle layers. These plexuses control the orderly peristaltic

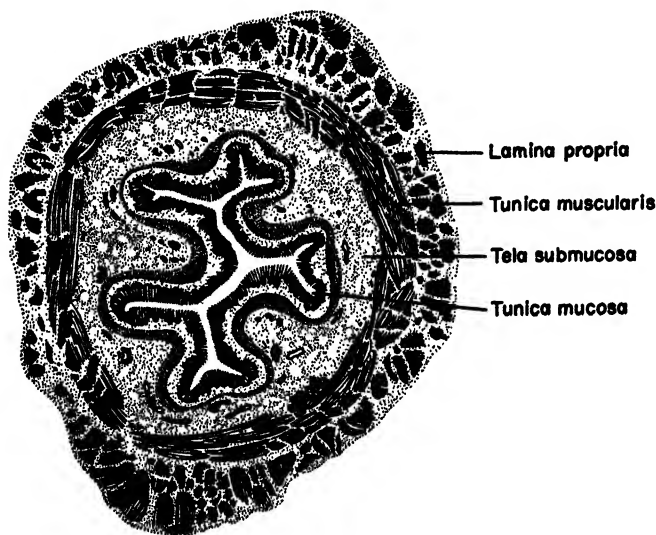


FIG. 177. Cross-sectional view of esophagus. This is a muscular tube consisting of a superficial layer, the lamina propria. Underneath the first is the tunica muscularis followed by the submucosal and mucosal layers. The latter is characterized by a squamous cell lining in the esophagus.

movements of the tube, even though their external nerve connections be cut. Since the esophagus is a connection between mouth and stomach, without digestive functions, absence of digestive glands other than lubricating glands is attributed to that fact. Unless food is passing through, the lining layers are closely approximated by folds of mucosa and submucosa. This folding is not communicated to the muscularis externa, which maintains the esophagus in a cylindrical form.

Histology of Stomach. The stomach is a specialized expansion or dilatation of the digestive tube. Its upper, or cardiac, end is a direct

continuation of the esophagus; its lower, or pyloric, end is continuous with the duodenum, the first division of the small intestine. The features of the stomach which strike the eye at first glance are its shape and the expansion. Immediately beyond the esophageal-cardiac junction a widened bulbous portion, the *fundus*, is raised above the level of the esophageal opening, and since the stomach is inclined to the left side of the abdomen, this fundic portion is in the epigastrium. The *body* of the stomach descends for a varying distance. This, with the fundus, is the most expanded part, and near its lower termination the wall is commonly somewhat notched by the *incisura angularis*, a definite notch or groove observed in many animals. The stomach makes a sharp upward bend from this angle, beyond which is the *pyloric vestibule*, *pyloric antrum*, and *pylorus*. A *greater*, or outer, and a *lesser*, or inner, *curvature* result from the nature of the stomach dilatation. In life the vascular supply, spleen, transverse colon, and mesenterial fat, in close proximity to the stomach, may almost obscure it.

The layers of the stomach are, beginning from without, the tunica serosa, tunica muscularis, tunica submucosa, and tunica mucosa. The first layer is an extension of the peritoneum lining the body cavity. The tunica muscularis has three layers of smooth muscles in contrast to the two in the esophagus. The outer layer is longitudinal and separates into two distinct groups of fibers. Beneath the longitudinal, the circular layer spreads uniformly over the stomach, except at the pyloric end, where its fibers are concentrated in a compact ring, the pyloric sphincter muscle. An inner oblique layer, better developed in the cardiac portion, may fade out near the pyloric end. Between the tunica muscularis and the mucosa, a submucosal or areolar layer of connective tissue connects the two. A muscularis mucosa, of smooth muscle fibers, also arranged into an inner circular and an outer longitudinal layer, separates submucosa from mucosa. Apparently contraction of the muscularis mucosa aids in the emptying of gastric glands. The gastric mucosa, or inner layer, which may be up to 1.5 mm. thick in the contracted stomach, is variously raised into folds; in the distended stomach these are smoothed out. The lining cells are a simple columnar epithelium.

Gastric pits open everywhere on the inner surface of the stomach and extend outward into the mucosa. They are continuous, with gastric glands at their bases, the latter extending even more deeply into the mucosal layer. The glands are tubular, and several commonly open into a single gastric pit. Maximow and Bloom estimate their number at 35 million in the human stomach. Their character differs in various regions of the stomach, although the nature of the pits is similar. Three

regions or zones are recognized with the following types: (1) cardiac glands; (2) fundic glands; (3) pyloric glands. The first include the area immediately adjacent to the esophageal opening; the second, the fundus and most of the body of the stomach; the third, the pyloric portion of the stomach. These glands, tubular in nature, contain four types of cells, named according to Maximow and Bloom:

1. Chief cells (zymogenic cells) in the lower part of the tubule presumably secrete pepsin in the presence of hydrochloric acid.

2. Parietal cells throughout the length of the gland are cells with large nuclei and characteristic intracellular secretory canaliculi; they secrete the precursor of hydrochloric acid, which is converted into free hydrochloric acid on the surface of the mucous membrane.

3. Mucous neck cells, in the necks of glands, presumably secrete mucus, forming a protective layer on the lining surface, and protect against autodigestion.

4. Argentaffin cells scattered in tubules, with unknown function.

Cardiac and fundic glands contain parietal, mucous, and chief, or zymogen, cells. Parietal cells are lacking in the pyloric glands, and some have questioned their ability to secrete pepsin. Adkins and Starling believe that they secrete a chemical excitant (gastric secretin), thus causing the liberation of gastric juice.

The vascular supply to the stomach is largely through branches of the celiac artery. The innervation is by the parasympathetic (vagus) and sympathetic routes, as it was in the esophagus.

The Small Intestine. The remaining divisions of the digestive tract are the small and the large intestine (Fig. 178). The small intestine is divided into three regions in man. The *duodenum* constitutes roughly the first 12 in. beyond the pylorus, the *jejunum* comprising two-fifths and the *ileum* the remaining three-fifths of the small intestine. The entire length of the small intestine is about 22½ ft. in the human male and slightly longer in the female. The character of the walls of the small intestine does not change markedly from region to region and with the exception of the oblique muscle layer in the stomach, which is absent in the small intestine, resembles that of the stomach. The character of the glands in mucosa and submucosa, however, changes definitely in comparison with the gastric glands.

The primate duodenum, the first division of the intestine, is characterized by extensive flexures which result in an almost complete circle in the interval between pylorus and jejunum (Fig. 179A, B). Superior, descending, transverse, and ascending segments are recognized. The ascending and duodenojejunal flexures are firmly tied to the body wall by

a *suspensory ligament*, also called the muscle of Treitz, since it may contain muscle fibers. The duodenum is further characterized externally by the opening of the *common bile duct* and *pancreatic duct* into the medial aspect of its descending arm. Internally, duodenal, or *Brunner's, glands* lie in the submucosa. They secrete a viscous alkaline fluid which contains an enzyme closely resembling pepsin when activated by hydrochloric acid. *Secretin*, a hormone produced by the duodenal mucosa,

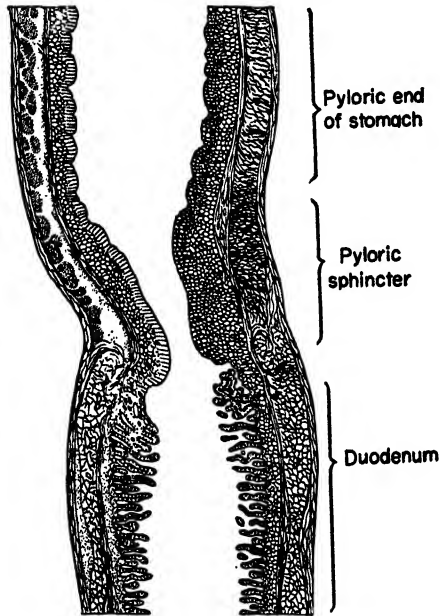


FIG. 178. The pyloric-duodenal junction in the rabbit. The mucosal layer of the duodenum is highly glandular. In addition to the layers observed in the esophagus, a serous membrane surrounds the lamina propria.

activates pancreatic secretion. In connection with its discovery in 1902, Starling first used the designation *hormone*.

The mucous membrane, greatly folded into circular valves or collars, juts into the intestinal lumen along with tiny, finger-like *villi*. Between the bases of the villi are the *crypts of Lieberkühn*. The surface of the villi is covered by a simple columnar epithelium in which goblet cells, chromaffin, and epithelial cells with cuticular borders are differentiated. The mucous secretion, as well as epithelial debris, contributes a considerable portion to the feces.

The crypts, or glands, of Lieberkühn are lined with columnar epithelium apparently in a transitional stage. Regeneration and renewal of goblet and columnar epithelial cells, destined for the surface of the villi,

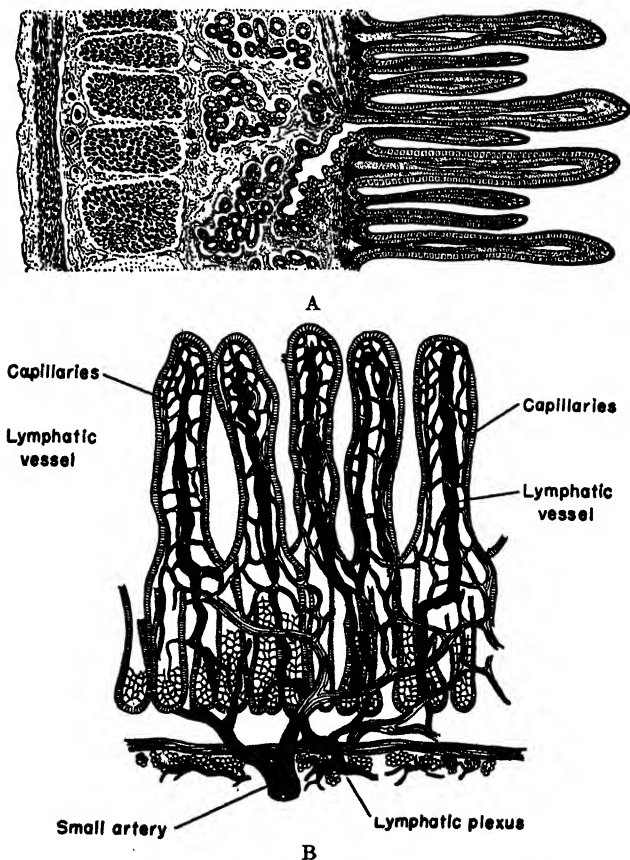


FIG. 179. A, the duodenum (cat). The duodenal lining is greatly folded. It contains specific (Brunner's) glands. Bile duct and pancreatic ducts open into it. B, detail of intestinal villi, blood and lymph supply. (After Gray.)

occur here. The intestinal juice, estimated at 3 l. a day in man, is secreted by these cells. The juice (*succus entericus*) elaborates several enzymes, including *erepsin* and *nuclease*, which act on proteins, converting them to amino acids; *lipase*, acting on fat; and *enterokinase*, which

converts starches to sugar. Besides the glands of Lieberkühn, *lymphoid tissue* in nodular aggregates is frequent throughout the small intestine and occurs to some extent in the large. Where these nodules are massed together, they form *Peyer's patches*, particularly in the ileum. These are areas infiltrated by lymphocytes and may be most marked in those regions of the ileum denuded of villi and epithelial covering.

The Large Intestine. The meeting point of large and small intestine, marked by a cecum, is known as the *ileocolic junction* (Fig. 180). A valve guards the union internally. The ileum enters the side wall of the colon and appears to push a part of that wall ahead of it, thus forming an upper and a lower fold, which guard the orifice. The longitudinal muscle layer of the intestine does not take part in this valve formation; the cir-

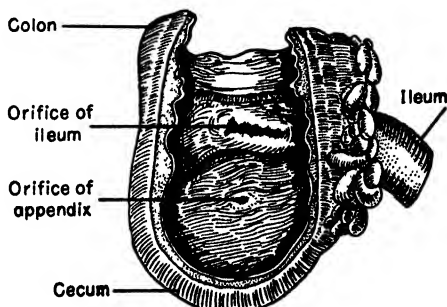


FIG. 180. The ileocolic junction. The junction of small and large intestine may be marked by a cecum and appendix as it is in the human being. An extensive pouch occurs in many ungulates. In many Cetacea the transition may be indiscernible to the naked eye.

cular, on the other hand, is continued in the body of the valves. Distension of the colon closes the slit between the two valve segments. The part of the colon below the orifice of the ileum is the *cecum*. In man it is about 2 to 3 in. long and has a diameter of about 3 in. In other mammals it may be very extensive. From the medial-posterior surface of the cecum the *vermiform appendix* originates and lies in varying positions in the lower right-hand abdominal quadrant.

The colon, from its junction with the ileum, ascends along the right side of the abdomen to the lower surface of the liver (ascending colon), where it makes a sharp turn to the left (right colic flexure) and passes across the abdomen. From the right flexure to the left flexure on the opposite side of the abdomen it is known as the transverse colon. The pancreas is attached to the latter by a mesentery, the transverse meso-

colon, and lies partly under cover of the stomach. At the lateral end of the spleen the colon executes a downward turn (left colic flexure) and descends along the left side of the abdomen as the descending colon. In the pelvis it is known as the pelvic, or sigmoid, colon (the latter because of its S shape); it passes into the rectum, which in turn opens into the short anal canal, whose opening, the anus, marks the termination of the tract. The colon in man is about 5 ft. long.

Structurally the large intestine shows a number of differences in comparison with the small (Figs. 181, 182). The serous layer does not com-



FIG. 181. The large intestine of the elephant. The sac-like large intestine of herbivorous animals may reach enormous proportions. Compare the size of the elephant cecum with the figures in the background.

pletely surround the ascending and descending branches of the colon or the rectum. The longitudinal muscular layer is not continuous but is arranged in three *flat bands*, a posterior, anterior, and medial. Because these bands are shorter than the underlying layers, they lead to sacculatation, giving the large intestine its characteristic appearance. At the rectum the bands become more or less continuous. Internally, villi are absent in the mucosa; crescentic folds in the mucosa, however, are retained. *Mucous glands*, very numerous and arranged in tubular fashion, open on the surface of the mucosa by small orifices. *Lymphoid bodies*, scattered throughout the large intestine, are extremely numerous in the

cecum and the vermiform appendix. Small outpocketings of peritoneum filled with fat, the *appendices epiploicae*, further mark the serous layer of the colon. The *rectum* is about 6 in. long and may be distended to a diameter of about 3 in.

Levator ani muscles surround the anal canal. These paired muscles, between the canal and the anal opening, reduce the opening to a narrow slit which is still further constricted by internal and external sphincter ani muscles. The canal is about $1\frac{1}{2}$ in. in length. Because of the up-right position which man has assumed, the muscles and fascia of the



FIG. 182. The intestinal tract of the finback whale. The animal was 71 ft. long and weighed 130,946 lb. The intestine measured 585 ft. in length and showed no division into small and large intestine upon gross examination.

perineum constituting the urogenital diaphragm are highly developed. The weight of the viscera, and in pregnancy the weight of the fetus, all rest on this diaphragm. In animals like the horse or cow a negative pressure may be exerted on these muscles since the weight bears down on the abdominal muscles.

GLANDS ASSOCIATED WITH DIGESTION

Associated with the digestive processes are glands in various locations and of varied types (Fig. 183A, B, C). They are best understood in light of the functions demanded of any gland involved in breaking down food.

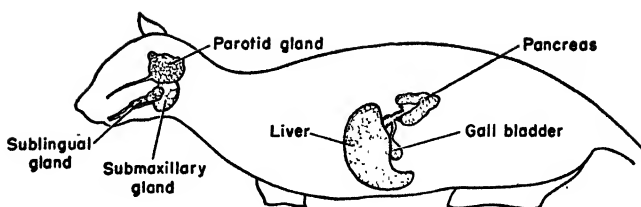


FIG. 183A. The extrinsic digestive glands of the cat. Parotid, submaxillary, and sublingual glands are associated with the mouth. Pancreas and liver pour their secretions into the duodenum.



FIG. 183B. Detail of mammalian liver. (Courtesy of Sharpe and Dohme.)

To serve these ends we find lubrication provided largely by mucous and in part by serous glands; addition of water by serous glands; breakdown of sugars and starches by salivary, pancreatic, and enteric glands; digestion of proteins by stomach and intestinal glands; emulsification of fats by enteric and pancreatic glands and by the liver.

Salivary Glands. Since food is taken in as carbohydrates, proteins, and fats, glands secreting enzymes become of primary significance. Salivary glands, absent in aquatic forms, include small labial and buccal, parotid, submaxillary, sublingual, and mucous glands associated with the

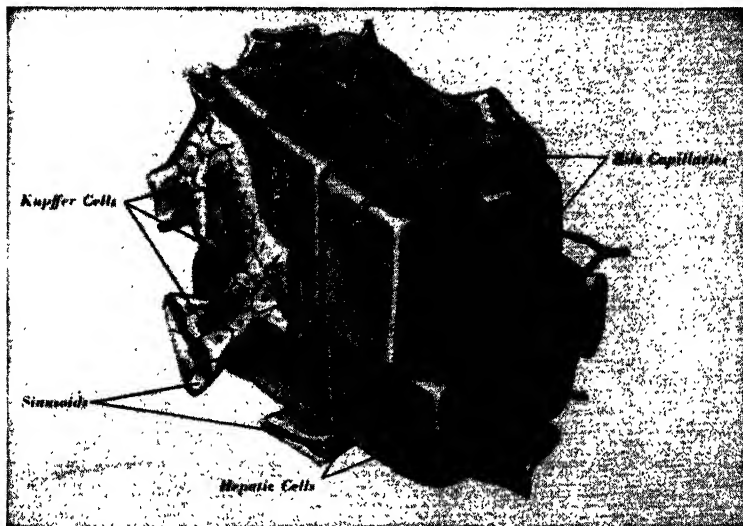


FIG. 183C. Histology of the liver. (Courtesy of Sharpe and Dohme.)

mouth in most land mammals. The *parotid glands* are the largest of the salivary glands. They lie just below and in front of the ear, encapsulated in a fascial covering. Running through the gland is the external carotid artery, the posterior facial vein, together with branches of the facial nerve. The parotid duct emerges from the anterior margin, crosses the masseter, pierces the buccinator muscle, and opens inside the cheek at the level of the second upper molar tooth. It is purely a serous gland in the adult, *i.e.*, its albuminous secretion is free of mucin, and mucous-secreting cells are generally absent. The gland, like the submaxillary and sublingual, is classified as a compound tubuloacinar gland, pouring

its secretions into a system of branching ducts that eventually lead into the main duct. The parotid duct is also known as Stensen's duct.

The *submaxillary gland* (mandibular) lies under the body of the mandible, and its duct (Wharton's duct) opens underneath the tongue at the side of the frenulum. It is a mixed gland, which means that it has both serum- and mucus-secreting cells. The *sublingual glands*, considerably smaller than the parotid or submaxillary glands, lie underneath the mucosa of the mouth and at the sides of the frenulum. The glands open via the submaxillary ducts as well as by numerous independent openings through the mucosa at the sides of the frenulum. In some rodents and ungulates the submaxillary glands are extremely large, implying a high degree of mouth digestion.

Besides these three pairs, smaller salivary glands are found in the vestibule of the mouth, in the buccal and lingual surface, as well as in the oropharyngeal mucosa. They are usually the mixed type.

The innervation of the salivary glands is autonomic. Sympathetic fibers reach the gland from sympathetic plexuses, originating in the cervical sympathetic ganglia, and from parasympathetic fibers, associated with the seventh and ninth cranial nerves. In the case of the parotid gland, a branch of the glossopharyngeal nerve, the small *superficial petrosal nerve*, passes to the otic ganglion at the upper border of the palatine canal. From the ganglion the nerve fibers destined for the gland pass with the maxillary division of the trigeminal nerve to reach the gland. The submaxillary and sublingual glands are supplied by sympathetic elements which accompany the entering arteries and by parasympathetic elements from the facial nerve. These pass by way of the *chorda tympani* nerve to the submaxillary ganglion and are distributed from that ganglion to the glands in question. The presence of secretory nerve fibers has been established in connection with the secretions of these glands. In many mammals these glands may be reflexively stimulated by the sight of food.

Salivary secretions contain, according to Howell, flat epithelial cells and altered leukocytes, mucin, the diastatic enzyme ptyalin, maltase, small amounts of protein, potassium sulfocyanide, potassium and sodium chloride, potassium sulfate, sodium and calcium carbonate, and phosphate.

Saliva, through the presence of ptyalin, converts starch to a polysaccharide sugar (dextrin and maltose). This is broken down to a simple sugar (dextrose) by the enzyme maltase in the small intestine. In this state it is absorbed and may again be built up into a polysaccharide in

the tissues. This is the only digestion that occurs in the mouth; the remaining functions of the salivary glands are associated with moistening, dissolving, and lubricating the food.

Liver. The glands of the esophagus, stomach, and intestine have already been described. There remain the pancreas and the liver, both involved in digestion, and both derived from the intestinal walls. In the human embryo of about 3 to 4 weeks the liver first appears as an outgrowth of the epithelial lining at the junction of the fore- and midgut. The primordium grows upwards to the septum transversum, which separates the heart from the abdomen. The liver buds grow into the septum and fuse with its vessels. With continued growth it appears to be suspended from the septum transversum. The latter becomes differentiated in the meantime into a lower portion, associated with the liver, and an upper part, the diaphragm. With its downward growth the liver pushes between the folds of the ventral mesentery, eventually separating that mesentery into a falciform ligament that attaches to the ventral abdominal wall, and into the lesser omentum. The lesser omentum extends between the lesser curvature of the stomach and the liver. The detailed relations of these mesenteries are described, beginning on page 342.

In the adult mammal, the liver lies in close proximity to the diaphragm and in man in the right side of the upper abdominal cavity. Its functional relationship to the intestine is maintained by the *bile duct*, which, as noted, enters the duodenum. This duct is known as the common bile duct. It should be remembered that the bile secretions formed in the liver are collected into *hepatic ducts* which open into the common bile duct, which leads to the duodenum. Leading from the junction of these two ducts, a *cystic duct* extends to the gall bladder. This means that bile secretions may pass along the hepatic ducts to the common bile duct and thence to the gall bladder by the cystic ducts. As the secretions are needed, they leave the gall bladder, which is simply a reservoir for bile, via the cystic and common bile ducts and pass into the duodenum.

The human liver varies considerably in weight, ranging from about 1,200 to 2,800 gm. in a series of human bodies in our collection, the weights taken at autopsy. In animals like the horse it is relatively small, weighing between 3,500 to 6,500 gm. in the full-grown animal. In the pig it weighs between 1,500 and 2,400 gm. It has a number of functions, including phagocytic properties of its reticuloendothelial cells, destruction of red blood corpuscles, formation of glycogen, and production of bile acids, urea, cholesterin, and lecithin. Early in life it forms

red blood cells. We commonly associate the liver with bile production, and this it does through its ability to utilize broken-down red blood cells. Active red cells show a low sedimentation rate; those destroyed by the liver have a high rate. The term *sedimentation rate* refers to the degree of rapidity of the sinking of the red blood cells in a quantity of drawn blood. Specifically, the Kupffer cells of the liver digest the red blood cells and convert hemoglobin to bilirubin and biliverdin, which then form the chief pigments in the excreted bile.

The relationship of the liver cells to the bile capillaries and ducts and to the vascular channels is best visualized in a histological examination of the gland (Fig. 183B, C). The liver consists of minute *lobules* about 1 to 2 mm. in diameter, maintained by delicate *areolar fibers*, which collectively are known as the *hepatobiliary capsule*. In the lobules the liver cells are arranged in columns radiating from the center to the periphery like the spokes of a wheel, save that the columns are closely packed. Between adjacent columns *sinusoidal spaces* permit the flow of blood from surrounding *interlobular veins* to a *central vein* at the hub of each lobule. Blood may come in close contact with the liver cells through the endothelial sinusoidal walls. Phagocytic cells of endothelial origin, known as stellate, or *Kupffer cells* and forming part of the reticulo-endothelial system, are in the sinusoidal walls. The columns of liver cells have minute channels within the columns, since a column consists of a double row of cells interrupted by a narrow space; these are the *bile capillaries*.

The chief blood supply to the liver is by way of the *portal vein*; the relatively small *hepatic artery* nourishes chiefly the gall bladder, walls of larger veins and bile ducts, and connective tissue. Draining the blood from the liver is the hepatic venous system to the inferior vena cava. Portal and hepatic branches remain distinct throughout. The branches of the portal vein assume interlobular positions and branch into the sinusoids between adjacent liver cell columns within the lobule. The sinusoids in turn enter the central, or intralobular, vein in each lobule, the latter belonging to the hepatic venous system. Thus, sinusoids form the communication between portal and hepatic vessels. To summarize: The blood enters the liver by the portal system, traverses the larger portal branches to the interlobular veins, and thence to the sinusoids; it goes from the sinusoids to the central intralobular, intercalated, and collecting veins to the large hepatic channels and to the inferior vena cava. The hepatic arterial blood ultimately finds its way into the sinusoids and thence to the hepatic veins.

The bile capillaries within the lobules have been mentioned. These interlobular bile canaliculi enter interlobular ducts between adjacent lobules, joining finally the large hepatic ducts, which fuse and open into the cystic duct as indicated. It will be noted that in contrast to the blood flow within the lobule, which is centripetal, the outflow in the bile capillaries is centrifugal. The gall bladder into which the cystic duct opens has a capacity of about 60 to 100 cc. in the human body. In general it is correlated with the size of the liver. It is absent in many animals, including the mouse and the horse. The mucosal lining is greatly folded. Beyond its function as a reservoir for the storage of bile and the rhythmic contractions which may be elicited from its muscular wall, no specific functions are known for the gland. The liver in the levels above the fishes, and probably in the latter, is innervated by sympathetic and parasympathetic nerves that reach the gland through the perivascular plexuses, chiefly of the hepatic artery. Both secretory and inhibitory fibers have been disclosed.

Pancreas. The pancreas is in part an outgrowth of the duodenum, and in part it is derived from the primitive bile duct. It is the second largest digestive gland, weighing from 50 to 170 gm. in man. It has endocrine functions through cells that discharge digestive enzymes into the pancreatic duct. The gland is acinar in type, and the secreting cells are clustered about a central lumen. Between adjacent cells fine secretory capillaries extend to the lumen. Most conspicuous within the cells are *secretory granules*, which vary in position and numbers depending upon the nutritional state of the animal. Stimulation of the cells may cause an almost complete disappearance of these granules. The gland opens into the medial wall of the ascending loop of the duodenum by the pancreatic duct (Wirsung) in common with the bile duct. This duct extends to the tail of the pancreas, where it takes origin from the junction of small ducts of the lobules. An accessory duct (duct of Santorini) is frequently present. It opens directly into the duodenum, slightly above the duct of Wirsung.

Islands of Langerhans. The islands of Langerhans are cord-like cell clusters between the alveoli. They possess a greater vascularity than the remaining cells, a frequent characteristic of endocrine organs. By special staining techniques, two types of cells, alpha or A, and beta or B, have been identified. According to Maximow and Bloom, the total island count in an adult human pancreas varies from 208,369 to 1,760,000. The island cells secrete the hormone insulin responsible for sugar metabolism.

The gland is supplied by parasympathetic and sympathetic nerves that accompany the splenic and pancreaticoduodenal arteries to the gland.

MESENTERIES

Before examining the tract in the vertebrate classes, it is desirable to consider the mesenteries of the pleuroperitoneal cavity, since they are essential tissues in the maintenance and support of the viscera.

It will be recalled that the celom, or body cavity, results from the splitting and separation of the hypomere; its visceral, or splanchnic, portion closely surrounds the endodermal layer of the gut, while its parietal, or somatic, layer lines the body wall. Above and below the gut the splanchnic mesoderm of either side joins, creating in this way a *dorsal* and a *ventral mesentery* whose middle section is traversed by the intestine (Fig. 170). During development the ventral mesentery disappears largely, except where it attaches liver and urinary bladder to the ventral body wall. The original single celomic cavity becomes subdivided ultimately into three sections, a pericardial, which contains the heart; a pleural, which surrounds the lungs; and an abdominal, which envelopes the viscera. In the fishes the heart is separated from the pleuroperitoneal cavity by a *transverse septum*; in other words, the original celom is now separated into two compartments. Beginning in the lunged amphibians, the heart descends ventrally and caudally and the lungs push into the pleuroperitoneal cavity dorsal to the septum, which, because of the migration of the heart, has assumed an oblique position. This is essentially the condition in the reptiles. In birds and mammals, separation of the lungs from the peritoneal cavity is completed by a celomic fold from the dorsal body wall which fuses with the transverse septum. In birds this dividing septum acts in a passive capacity to separate the three groups of organs, heart, lungs, and viscera, while in mammals the muscular diaphragm at this site becomes an active part of the breathing mechanism. The liver remains attached anteriorly to the transverse septum or to the diaphragm, as the case may be. A constriction at its junction with the diaphragm marks the coronary ligament.

With the great increase in length of the intestinal tract, beginning particularly in the Amphibia, the mesenteries supporting its various divisions likewise increase in extent. Examination of these mesenteries in the adult alone leaves but a confused picture; in the light of their embryology the relationships become evident. The *dorsal mesentery*, from which various specialized mesenteries are derived, does not extend without interruption along the dorsal line of the pleuroperitoneal cavity

either in the fishes or in the abdominal cavity of mammals; in the region of the small intestine particularly it is considerably modified. Supporting the stomach is the *mesogaster*, which also continues around the spleen; the narrow mesenteric fold which thus ties stomach to the spleen is the *gastrosplenic ligament*. The dorsal mesentery proper ties the small intestine to the dorsal body wall.

The interrupted dorsal mesentery, referred to in the preceding paragraphs, may be absent in certain elasmobranch fishes. In birds and mammals it is particularly well developed, correlated with the increased length and coiling of the small intestine; in the human being it may reach a length of 6 m. As indicated, the *ventral mesentery* is greatly reduced and consists of two divisions, the *gastrohepatic* and the *hepatoduodenal ligaments*, joining the stomach, liver and duodenum, and known collectively as the gastrohepatoduodenal ligament, or *lesser omentum* (Fig. 184). The gastrohepatic ligament unites the liver and the lesser curve of the stomach; the hepatoduodenal, the liver and duodenum. The portal vein traverses the ligament in its ascent to the liver, and the bile duct descends within its folds to the duodenum. It is represented in the remaining vertebrate classes. A *coronary ligament* unites the liver with the diaphragm and a *falciform* joins the liver to the ventral body wall. In birds, associated with the grinding stomach, or gizzard, is a ventral ligament continuous with the falciform ligament midventrally and anchoring the gizzard to the ventral body wall. That part of the dorsal mesentery supporting the large intestine and uniting it with the dorsal body wall is the *mesorectum*, which in mammals receives special designations, *transverse* and *sigmoid mesocolon*, depending upon the part of the colon to which it is attached.

Supporting the ovaries are *mesovaria* confluent with *mesotubaria* that attach the oviducts to the body wall in the female. A *broad ligament* extends from the oviducts to the body wall in the mammalian female, while the *round ligament* on either side of the uterus ties that organ to the margins of the pelvis. *Mesorchia* attach the testes to the body wall where these organs are internal. If they descend outside the abdominal cavity, they carry the peritoneal sheath ahead of them and remain enveloped within the resulting pouch.

COMPARATIVE ANATOMY OF THE DIGESTIVE TRACT

Regardless of the system under comparison, in the advance from lower vertebrates to man we are confronted with an orderly and correlated series of adaptations leading to specific levels of being. The digestive tract is no exception, and it manifests in very clear fashion the concept

that individual systems proceed to certain levels of organization and remain apparently fixed at those levels. There is no mistaking the digestive tract of a fish, a bird, or a mammal. Each, while it conforms in its wholeness to a digestive tract, remains distinctive for its class. The peculiar ventriculus and the absence of teeth, characteristic of the bird; the obvious and functional streamlining of the snake tract; the addition of mouth glands, special mesenteries, and other adnexa in the land mammal, all related in their functions and structures to other systems in these classes, give evidence of continuous correlated adaptations.

Specifically how does this system change from class to class? The following is a brief survey of the system in the various classes.

Amphioxus, representative of the protochordates, has a very simple tubular digestive tract. The mouth, as already noted, is cone-shaped, without lower jaws. The oral hood provided with cirri at the outer margin of the cone leads to a wheel organ on its inner surface. The latter is at least partly ciliated. A velum, or thin vertical membrane, carrying small velar tentacles, surrounds the mouth opening posterior to the wheel organ. This leads into the elongate and expanded pharynx already described. The latter is the common channel for water as well as for food particles.

Beyond the pharynx, which extends about half the length of the body, a very short esophagus leads directly into another expanded portion of the tube, the stomach, from which a characteristic ventral diverticulum, the liver, is directed anteriorly. Beyond this the intestine extends caudally to the anus. Both liver and digestive tube secrete digestive enzymes. The intestine is without loops and appears as a tube within the larger, or body, wall. The dorsal wall of the pharynx carries an epipharyngeal ciliated tube that connects anteriorly with paired ciliary bands arranged along the pharyngeal wall from the floor of the pharynx to the epipharyngeal groove. Small food particles taken into the pharynx and collected in the endostyle along its floor are directed upward into the epipharyngeal groove and into the intestine. The movement of food is directed by cilia throughout (they set up water currents), and absorption of the particles, broken up by the enzymes, occurs in the epithelial cells of the intestine.

The *ammocoetes larva* of the cyclostome is more typical of primitive vertebrate structure than is *Amphioxus*. In its digestive tract, however, it shows considerable superficial resemblance to that of *Amphioxus*. An oral hood leads into the mouth. It will be recalled that in the adult cyclostomes the cone-shaped mouth without lower jaw has horny teeth not comparable with the true bony teeth of the fishes. A velum sepa-

rates the mouth from the pharynx. In the adult lamprey the mouth opening leads into a buccal cavity from which esophagus and pharyngeal tube extend caudad, the latter ventral to the esophagus. The stomach is a slight enlargement near the anterior end of the tract. The intestine extends as a tube to the anus. Ciliary action conveys the food as it did in *Amphioxus*. Above the cyclostomes, cilia are restricted to pharyngeal levels, and food is pushed along the tract by peristaltic action. The cyclostome liver has a single lobe. A gall bladder occurs in the larva, but disappears after metamorphosis. Neither a pancreas nor a spleen is defined. Associated with the liver are small cell aggregates which have been termed the pancreas. Enzymes produced by the epithelial intestinal lining and by the liver place the food in solution. Paired glands associated with the mouth have been termed salivary glands. The tongue is a rasping organ supplied with two rows of minute teeth, and the mouth opening and tongue are supported by an annular cartilage.

The **fishes** show a marked departure in the architecture of the mouth, in comparison with the protochordates and the cyclostomes. With addition of a lower jaw, the mouth has become an active agent in the procurement of food. This permits larger amounts to be gathered than are taken in by ciliary action, and with addition of bony teeth the mouth further enlarges its activities by becoming a means of offense and defense.

In the **elasmobranch fishes** the **mouth**, without salivary glands, leads to a wide *pharynx*, the latter in communication with the outside by gill slits. This is in contrast to the cyclostome pharynx, which is quite separate from the gullet and which ends blindly ventral to the esophagus. The elasmobranch *esophagus* is very short and is best identified by the numerous papillae in its walls. The esophagus leads almost immediately into an expansive J-shaped *stomach*, which terminates in a narrowed *pylorus* (Fig. 184). The latter becomes quite muscular through development of a circular smooth muscle layer about the stomach and emphasized about the pylorus. While differentiation of the tract has not proceeded far, a *duodenum* is recognized immediately caudad to the pylorus. Into it open the pancreas and the liver by the pancreatic and *bile duct*, respectively. The duodenum is very short. In an 8-ft. shark it is only about 6 to 8 in. in length. It is continuous with the *valvular intestine*, so called because of the *spiral valve*, or fold, that spirals about an imaginary center in the middle of the intestinal lumen, with its margins attached along the inner surface of the intestinal wall. Circular arteries and veins in the outer intestinal wall mark the line of attachment of this spiral fold. The valvular intestine communicates with a very short *large intestine*, again but a few inches in length in a large shark,

and terminating in the anus. Associated with the large intestine by a small duct and lying in the body cavity is a *rectal gland* of unknown function. Most prominent in the abdominal cavity, unless the stomach is overfilled with food or the animal is pregnant, is the *liver*, an elongate bilobed organ usually weighing two to four times as much as the entire

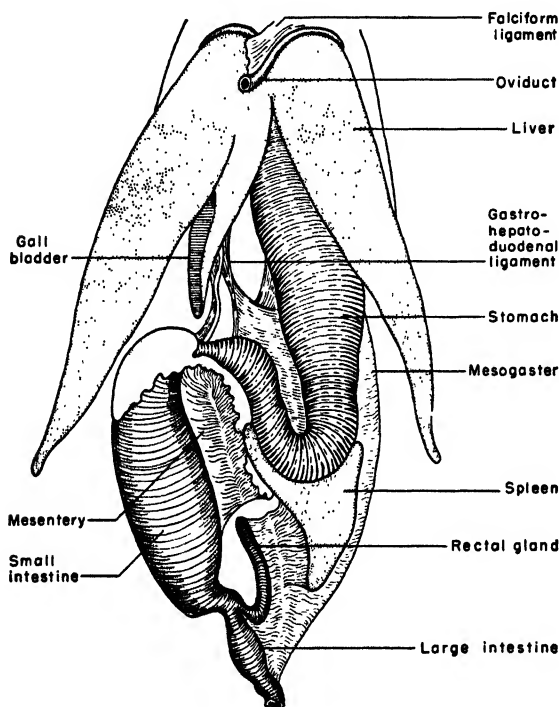


FIG. 184. The intestine and mesenteries of the dogfish. The intestine of all vertebrates is tied to the body wall by mesenteries. These receive distinctive names depending upon the structures to which they are attached.

intestinal tract. The median lobe has a *gall bladder*, partly embedded within, and originating from the bladder an elongate *bile duct*, the latter carried in an extension of the ventral mesentery, the *gastrohepatic ligament*. Its opening has been noted.

The *pancreas* is elongate and of two lobes, a ventral and a dorsal; the former lies in the curve of the duodenum, the latter dorsal to both stomach and duodenum. The *spleen*, a dark-red, triangular vascular organ,

is attached to the convexity of the stomach by a mesentery but has no direct functional relations to the digestive system. Salivary glands are lacking; the food is swallowed, sometimes in very large pieces; in fact, entire fish of considerable size may be conveyed to the stomach and left to the rapid disintegrating powers of the gastric secretions. Digestion seems to take place almost entirely in the stomach, while absorption occurs in the valvular intestine. The spiral valve, or fold, already described, increases greatly the absorptive powers of the tract; it aids further in the retardation of the passage of food and through its relatively high degree of vascularity is probably the functional equivalent of a longer intestine without this absorptive fold.

The digestive tract of the **bony fishes**, although considered a rather simple system when compared with the mammalian, nevertheless has the same essential functions and abilities. The chief distinctions appear in the degree of differentiation of its several parts.

The esophagus is short and lined anteriorly with papillae; its wall is largely of striated muscle. In some fishes this striated muscle may extend over a large part of the intestine. The stomach is J-shaped and relatively large and glandular in the elasmobranchs, while in the dipnoan fishes it is straight and only slightly expanded. In some of the bony fishes a differentiation has occurred between the fundus and the pyloric glands. In the Cyprinidae, according to Ihle, a stomach is absent, and the esophagus connects directly with the midgut at the level of the hepatic duct.

The midgut, or small intestine, traditionally the site of digestion and absorption as well as the site of origin of pancreas and liver, continues to receive ducts from these glands. Characteristically its mucosal lining is folded. In the cyclostomes this folding is longitudinal, with some evidence of spiraling. In the elasmobranchs, as noted, a spiral fold, well supplied with blood vessels, is an outstanding feature. In many of the teleosts this spiral does not appear. Pyloric appendices or ceca may be associated with the anterior end of the small intestine, particularly in the codfish. Presumably these ceca have a digestive function, since glands have been noted in their mucosal lining. At the terminus of the small intestine a direct transition to a short end gut or large intestine occurs. In some of the bony fishes, however, a definite ileocolic junction, marked by a valve, has made its appearance. A rectal gland of unknown function, mentioned earlier, commonly opens into the large intestine. In the Holocephali the anus has become separated from the cloaca to open independently to the outside.

The **frog** esophagus is short, highly distensible, and glandular (Fig.

185). The presence of digestive glands in the esophagus represents a peculiar condition not generally met, although the bird crop represents an analogous condition. Longitudinal folds originating in the esophageal mucosa extend into the stomach but no marked constriction occurs at the union of esophagus and stomach. The pyloric end, however, is marked by development of the circular muscle layer into a pyloric valve. The stomach lies to the left of the midline and is connected with the dorsal body wall by the mesogaster. The stomach lining is glandular, the upper end distinguished by the cryptic type of gastric gland. In this type the mucosa has evaginated into elongate outpocketings; its secreting cells arranged in tubular fashion open into the crypts. Near the pyloric end the character of the glands changes, and the cells correspond more nearly to those segregated at the upper ends of the cryptic glands. The secretions are acid in contrast to the alkaline character of the esophageal secretion.

The **amphibian** small intestine is differentiated into a duodenum and ileum, the former receiving the common bile duct. It also receives several small ducts from the elongate pancreas, located between the stomach and the duodenum. In comparison with the stomach, the small intestine is of relatively small diameter in the Amphibia. The mucosa is lined with goblet cells, which secrete mucus, and with absorptive cells. The former have a characteristic goblet shape with the nucleus near the base; the absorptive cells are narrower than the former, with oval nuclei at their bases and with thickened outer free borders. The blood supply is relatively copious to the small intestine. In urodeles, Lieberkühn's glands, characteristic of the mammalian small intestine, occur. In other Amphibia these are lacking.

The large intestine, short and thick-walled, has a folded lining whose epithelium is provided with mucus-secreting goblet cells (Fig. 185). In the naked *Gymnophiona* no differentiation is evident between the ileum and the large intestine. In all Amphibia the large intestine opens into the cloaca.

A sharp demarcation between esophagus and stomach is not general in the **reptiles**. The stomach is deflected to the left. The stomach musculature shows relatively greater development of the circular fibers than longitudinal. A definite pyloric valve occurs. The esophagus of the snakes is characterized by extreme elongation as well as by great distensibility, conforming with the shape of the body and the food habits of the animal. This lengthening includes the stomach and the small intestine. In the *Crocodylia* the stomach, through proximity of the esophageal entrance to the pyloric exit, appears sac-like and distended.

A small evagination near the pylorus indicates the beginning of an accessory stomach.

The reptilian small intestine in addition to its elongation exhibits greater coiling than was observed in the Amphibia. This holds particularly for the Chelonina and Crocodilia. An ileocolic valve separates the small from the large intestine, and a cecum marks the beginning of the

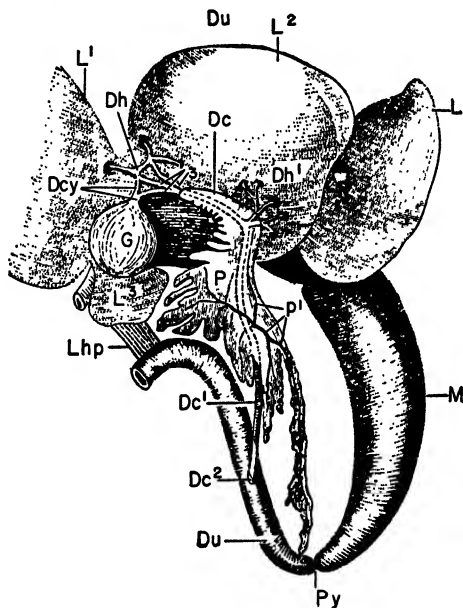


FIG. 185. Liver and pancreas of frog. Dc, common bile duct; Dcy, cystic ducts; Dh¹, hepatic ducts, which with the cystic ducts combine to form the common bile duct; G, gall bladder; L, L¹, L², L³, lobes of the liver turned forward; Lhp, hepatoduodenal ligament; M, stomach; P, pancreas; P¹, pancreatic ducts entering the common bile duct; Py, pylorus. (After Wiedersheim.)

large intestine in some. Paired anal bursae occur in the turtles. These are cloacal outpocketings with muscular walls and lined with epithelium. Their function is unknown. The large intestine is short and opens into the cloaca. The latter may be further differentiated into a proctodeum, into which opens the large intestine, and a urodeum, which receives the urinary ducts.

The bird esophagus, in contrast to that of other vertebrates, has an outer layer of circular muscle and an inner one of longitudinal fibers.

The esophagus is relatively long and may have an expansion the—crop, about halfway between the esophageal origin and terminus. The *crop* of grain-eating and carnivorous birds shows considerable modifications in various species. In the duck and the cassowary no secretions occur, while in the doves it is lined with glandular epithelium and is responsible for the elaboration of "pigeon's milk." Young squabs are nourished by the broken-down epithelial cells of the crop lining, which undergo fatty degeneration when the pigeons have young and produce the so-called milk. The normal secretions also function in softening the hard cellulose covering of grains, causing the seeds to swell and break their coverings. As a result of the fermentation of the food, acids are liberated which are active in digestion.

The bird stomach is clearly differentiated into a glandular *proventriculus* and into a mechanically acting muscular *ventriculus*. The latter occupies a large part of the abdominal cavity. Its lining is keratin-like, owing to the hardening of the gastric glandular secretions. This false lining may be raised into slight transverse folds and, upon addition of gravel, acts as an effective mill when food is supplied. The carnivorous birds in contrast usually possess a sac-like, expanded ventriculus. Fish eaters exhibit a large glandular proventriculus. Apparently the grinding action of the ventriculus substitutes in part for the loss of teeth.

The bird duodenum is elongate and expanded. Its U-shaped form encloses within it the pancreas. The intestine is of variable length even in birds within a single order. The mucosa, variously folded, frequently leaves traces of an earlier longitudinal furrowing. A diverticulum about midway along the small intestine persists in many swimming birds. In the ratite birds it may be retained as a small outpocketing throughout life. It corresponds to *Meckel's diverticulum* met with occasionally in the adult mammalian intestine.

The avian large intestine is short and opens into the cloaca. In the absence of a urinary bladder both excretory and fecal wastes are discharged directly into it. *Coprodeum*, *urodeum*, and *proctodeum* are differentiated in the cloaca. The first marks the terminus of the large intestine; the second receives the ducts opening from the kidney and the oviduct or vas deferens; the proctodeum is the common cloacal channel leading to the anus.

The human intestine has been described. The tract of the remaining mammals follows in general plan that of the Primates. In a number of details, however, they depart from this pattern, and where such changes occur they are correlated with the peculiar food habits of a particular group. The greatest modifications within the order appear in the char-

acter of the stomach, the length and differentiation of the small intestine, and the occasional appearance of intestinal ceca.

The *mammalian esophagus* is definitely marked from the stomach (Fig. 186). It passes through the diaphragm and almost immediately joins the cardiac end of the stomach. The upper end of the food tube has a striated muscular wall; the lower portion is smooth muscle. The

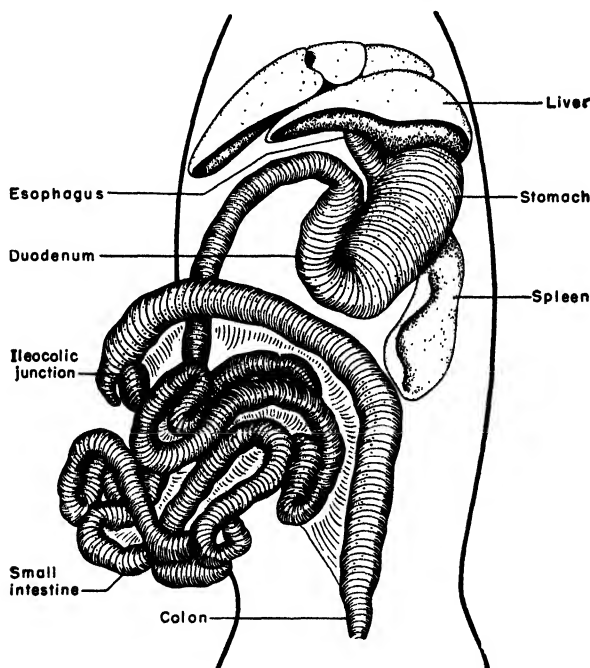


FIG. 186. The digestive tract of the cat. The cat has a well-differentiated alimentary canal. The large intestine is relatively more muscular in the Carnivora than in herbivorous animals.

stomach, more or less transversely placed, is differentiated into cardiac, fundic, and pyloric divisions, each characterized by specific glands. A well-defined notch, the *incisura angularis*, partly separates cardiac and pyloric portions in many marsupials, rodents, and primates. In the Cetacea, Sirenia, and Ungulata, this separation of the stomach into compartments has gone much further than in the Primates. The first two divisions of the ruminant stomach, for example, are expansions of the esophagus; they are lined with squamous epithelium as is the esoph-

agus. The homologue of the secreting and digesting stomach is represented by the last two divisions.

The four compartments of the ruminant stomach, and with some modifications the sirenian (sea cow) stomach, are designated by the following names and functions (Fig. 187). The first, or *rumen*, an esophageal expansion, lined with squamous epithelium, is a temporary storage space. Food is moistened and hastily swallowed, and the rough herbage which is its chief constituent is carried to this division. From here it passes to the second stomach, the *reticulum*, also an esophageal derivative, with a

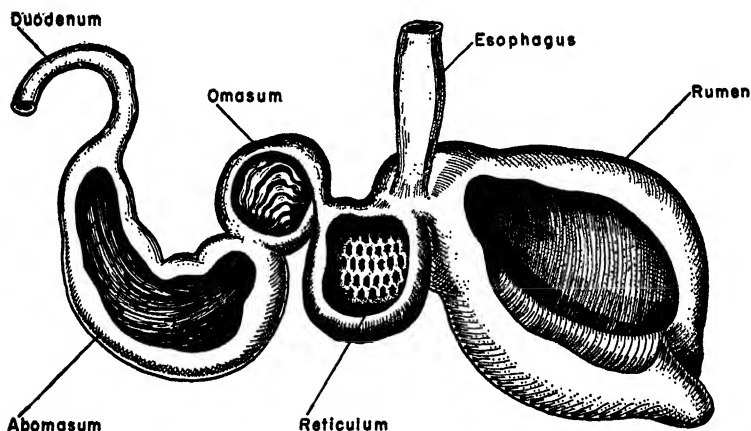


FIG. 187. Four-compartment stomach. This type of stomach, characteristic of ruminants, permits temporary storage in one compartment. Following regurgitation the food is digested and partly absorbed in the third and fourth compartment.

net-like mucosal lining and with pits within the meshes of the network. The moistened food is macerated by muscular action in the reticulum, partly fermented, and formed into cuds. The cud is regurgitated and chewed at leisure, whereupon it descends the esophagus for the second time and by-passes the rumen by entering a short trough at the lower end of the esophagus. This trough is formed by valve-like folds of the esophageal lining. Rough herbage, when it descends the esophagus the first time, depresses the folds of the trough and thus passes into the rumen. Upon the second downward passage the macerated and slippery food mass enters by way of the trough into the third division, the *omasum*. Muscular action of the omasum compresses and breaks down the mass

further, permitting the liquid portions to be absorbed, while the more solid fractions enter the *abomasum*, or glandular stomach. In the abomasum, chemical digestion takes place because gastric secretion is largely restricted to this division although some digestive glands are found in the omasum. In the camel the pits of the reticulum are developed into small water cells, or reservoirs, upon which the animal may draw in time of need. Some other animals show modifications in this respect; thus the giraffe is able to go without water for several days, apparently through ability to store water in this stomach lining.

The small intestine, the longest division of the tract, is the site of digestion and of absorption. It is generally longer in herbivorous than in carnivorous animals, although the seal, which is a carnivore, exhibits considerable intestinal length in comparison with land carnivores. A bearded seal of 110 lb. weight in the author's collection had an intestinal tract 71 ft. long. In a porpoise of 314 lb. body weight the author noted an intestinal length of 84 ft.; in a sea cow of 935 lb. it was 78 ft., while in one cetacean of 130,000 lb. it was 585 ft. and of even diameter (8 to 10 in.) throughout (Fig. 182). Ihle states that in cattle the ratio of small-intestine length to body length is as 20:1; in the horse it is 12:1. This ratio is greater than it is in the above-mentioned cetacean with a body length of 71 ft., or a ratio of approximately 9:1.

Transverse folds terminating in microscopic villi protrude into the lumen of the tract and increase the absorptive surface in all mammals.

Ceca at the junction of the small and large intestine occur in a number of animals with herbivorous food habits. Among these are the cony (*Hyrax*), rabbit, pig, and horse. Invariably in the living state the ceca are filled with partly digested food. Their function is absorptive; cellulose digestion apparently occurs here as well as in the colon, owing to a rich bacterial flora capable of breaking down the cellulose. The vermiform appendix, not to be confused with these digestive ceca, has a rich supply of lymph glands and lymphocytes that point primarily to bacteriophagic functions. In the porpoise, sea cow, and whales, the small intestine passes into the large without noticeable transition.

The colon in mammals is relatively short in comparison with the small intestine (Fig. 186). The sacculations called *haustra* and the *taeniae*, or longitudinal muscle bands, have been pointed out in connection with the description of the human tract. In ungulates and carnivores the longitudinal muscle layer is continuous, and consequently the *haustra* and *taeniae* are absent.

In the pelvis the colon terminates in the rectum, which is character-

ized by thicker and more muscular walls than the colon. The rectum terminates at the anus, or vent, supplied with specialized sphincter muscles.

SIDELIGHT

The hyena is a carrion feeder and a grave robber. The lion may resort to these tactics upon occasion or when old age makes it difficult to capture wild prey. Zebra and gazelle have learned to eat and run; the buffalo and elephant store great masses of grasses or leaves and twigs in their enormous paunches. We removed a mass of 380 lb. of such food from a 1,900-lb. African buffalo and a mass of 832 lb. from the paunch of a 14,640-lb. African elephant. Smaller food masses of 30 to 60 lb. in the paunches of the zebra were not uncommon. The lion, on the other hand, travels lightly so far as undigested food is concerned. Invariably we found its stomach empty. These animals were obtained while they were hunting for food, and this may explain the empty stomachs; zebra, buffalo, and elephant were also interrupted while grazing.

Digestion undoubtedly is more rapid in the carnivorous forms than in the herbivorous. This was further substantiated by examining the stomachs of freshly killed white whales in the arctic and porpoises off the Florida coast. These animals live on fish which they capture, and there is a saying among the Eskimos that no one has ever found food in the stomach of the white whale. Examination of several within half an hour after harpooning them in no instance disclosed more than a few skeletal fragments and scales of fish, although all animals were taken when they were pursuing and presumably feeding on fish. The stomachs of the great humpback and sperm whales were partly filled with "krill," small crustaceans quickly converted to a reddish "soup." This reddish fluid filled 200 or 300 ft. of the intestinal tract.

At nightfall we tied a "kill" to the end gate of our truck. This kill consisted of the dissected muscular and skeletal remains of a zebra upon which we had been working. The great brooding Althai plain, ringed by ancient volcanic peaks, stretched before us in the tropical darkness. No evidence here of the hunter or the hunted. When we stopped the machine for a moment, not a sound was heard save the chanting in a native village some distance away. And yet we could sense activity, for this is the time when jackal, hyena, and lion are on the prowl. Continuing across the plain, we swept the area about us with powerful flashlights, and we did not have long to wait before hungry hyena eyes were reflected in the beams. Within half an hour we counted 42 pairs of eyes by their reflections. The animals became bolder, some hot on the trail of the kill, others running parallel with the car; in the distance late-comers, attracted by the scent and perhaps by the barking of the nearby followers, joined the pack. Hyenas which we never observed in the daytime were here in great numbers. Cutting the rope that tied the kill to the truck and swinging the machine quickly about, we held them in the rays of the headlights and observed the hyena at the feast.

Packed in, one over the other, each tried for his share of food; they exemplified the primitive satisfaction of hunger. Three jackals appeared, and our guide whispered that lions must be near. A deep cough announced Leo's presence. Hungry and ravenous as were the hyenas, they ceased eating as if by command. Standing at attention for what seemed a minute, they continued their feast when the growl was not repeated. Their respect for the lion was obvious. Unfortunately he did not appear, and although he growled from time to time, the headlights kept him at a distance. In a few minutes the hyenas had finished the meal; some with bits of skeleton and tissue retreated to the darkness, and the remainder were scattered by fire from our rifles. These animals were not killed wantonly; the three hyenas shot on this occasion were dissected the following day.

After taking the hyenas, we made a short excursion to the area some distance around the truck. The activity in this circle of semidarkness and darkness was astonishing. Forms never or rarely seen in daylight were picked up by the flashlights; most astonishing of all was the curious springhaas, the jumping hare. This rodent, about the size of a large cottontail rabbit, has lost the use of his front limbs for locomotion, and he hops about on greatly developed hind limbs much as does the Australian kangaroo. The forepaws are flexed and held close to the body while he hops about. His long tail, measuring over 14 in., is another unexpected feature of this rodent. How he survives in the midst of the great assemblage of hungry carnivores is a mystery; his nocturnal activity particularly seems entirely out of keeping with the traditional timidity of the hare.

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CHAPTER 9

THE RESPIRATORY SYSTEM

PRINCIPLES INVOLVED

The term *respiration* means breathing, *i.e.*, permitting water to pass through specialized semipermeable membranes in gill-bearing animals, with consequent absorption of dissolved oxygen; or, with similar consequences, drawing air into and expelling it out of the lungs in lung-bearing animals. It also includes oxygen and carbon dioxide exchange within the tissues. Breathing implies that air and water have life-giving qualities, or that gills or lungs liberate toxic products which are expelled in breathing, or both. The latter inference is correct, for both inhalation of oxygen, the life-giving substance, and exhalation of carbon dioxide, the toxic product, are essential in breathing.

When the history of respiration is examined, we find that in the complex and integrated organ systems of the metazoan animal, respiration involves taking in of oxygen, its transport to the tissues, and its final delivery to all living cells. This at once implies an associated system, the vascular tree, to make breathing effective. The insects have eliminated some of these requirements in part by means of tracheal tubes which carry gases directly to or from the tissues. Required in the vascular tree are carriers for oxygen and carbon dioxide. The breathing apparatus antedates the circulatory system. In single-celled animals or in primitive multicellular ones the cell membranes are not far removed from the source of the oxygen supply. With equal ease, the carbon dioxide may pass into the immediate aquatic environment. Time, through natural selection, permitted the development of a circulatory system which, in addition to its plasma content, holding but a small amount of oxygen, also evolved the unique red blood cell, which not only took up oxygen as it was offered but was able to give it to the tissues requiring it. With this remarkable function it combined the converse ability of taking carbon dioxide from the tissues and delivering it to the surrounding water or air.

Living systems, in their growth and evolution, never ran counter to the physical and chemical laws which govern matter or control the distribution of energy. When the terms *diffusion*, *osmosis*, and *permeability*

are mentioned, many a student instinctively shudders and turns away from what may appear a forbidding subject. Actually these principles are basic to the existence of life as we understand it, and their consideration should give the student no cause for fear. Without their operation, breathing, digestion, excretion, release of energy in the body, and nervous activity are impossible. This means that respiration, digestion, and excretion, for example, have a number of basic functions in common.

What is meant by diffusion, osmosis, and permeability, and how do they apply to the function of breathing?

When two or more gases or liquid solutions are placed in a container so that the gases may circulate freely or, in the case of liquids, the substances in solution are unimpeded, the molecules of the gases will disperse evenly in the container and the molecules of the liquids will be evenly distributed after a time. This phenomenon of molecular dispersal is *diffusion*. If free movement of the molecules or ions of two solutions of different concentration is prevented by a separating membrane permeable to water, the latter will pass from the fluid of lower concentration to the higher through the membrane. The passage of the solvent through such a membrane is *osmosis*. If, for example, a cane sugar solution is separated from water by a membrane permeable to water but impermeable to sugar, water will pass into the solution. If the container of the sugar solution is connected with a mercury manometer, the water will enter the solution and cause the mercury to rise until the pressure of the column prevents further entry of water. The point of maximum rise under these conditions is the osmotic pressure of the sugar solution. This pressure varies with the concentration of the sugar solution as well as with the temperature. Increase of both factors increases the osmotic pressure. It also varies with the solute.

Permeability refers to the pervious nature of many membranes. One characteristic of animal cell membranes and of plant cell walls is their selective permeability, and on this factor hinges their significance to the cell. Membranes indiscriminately permeable to all crystalloids and colloids would be of little value in the maintenance of protoplasm. For food and oxygen intake and carbon dioxide and nitrogenous excretion, selective permeability of the cell membrane is a prerequisite.

Different solutions, as indicated, exert different osmotic pressures; those exerting pressures similar to the pressure within the cells concerned are called *isotonic*. For example, the cells of the body exhibit approximately the same osmotic pressure as does the blood; hence the two are isotonic. Fluids or gases introduced into the body, if they have a lower osmotic pressure than the red blood cells, are *hypotonic*; those with higher

osmotic pressures are *hypertonic* to them. These terms apply not only to solutions in relation to blood but to relationships between solutions and tissues. .

If a hypertonic salt solution, for example, is placed in the blood, the red cell shrinks in conformity with the principles of osmosis, since its osmotic pressure is higher than that within the red blood cell; and because the membrane is permeable to water, the latter passes from the blood cell into the hypertonic environment. Conversely, a weak salt solution, hypotonic to the red cells, has a lower osmotic pressure than that within the red blood cell, and water passes into the more concentrated solution within the blood cells. If these phenomena are thought of in connection with the water concentration in the two solutions, they may be more readily visualized. In both instances water passes from the region of its greater concentration to the region where it is less concentrated. It should be remembered also that solutions may be in an ionized as well as in a molecular state and that charged particles, just as molecular solutions, may traverse membranes.

What is the relationship of hypertonic, isotonic, and hypotonic solutions or osmotic pressures to the taking in of air? What do these phenomena have to do with breathing? The answer may be given in one word—everything. The tissues and secondary structures of the respiratory system depend upon the indicated physical phenomena to make breathing possible.

FUNCTIONS

The development, modifications, and refinements of various chordate breathing devices are best understood when the basic functions of the animal are explored. What can the biologist say or establish concerning these functions? The theologian has a positive and disarming answer to the question, "What is the function of Man?" (or of animal creation). He replies, "The glorification of God." The biologist, on the other hand, states that the functions of the animal are those of self-maintenance, of utilization of energy, and of reproduction. We shall concern ourselves here briefly with the second indicated function, the utilization of energy. Almost every bodily system implies this function; skeleton, muscle, digestive and nervous system—all are adapted to use energy in some form, harness it and transform it into work, heat, electrical or radiant energy.

Since the great source of energy in the body results from oxidation and since oxidation depends upon the union of the element oxygen with carbon, it is obvious that a means of capturing oxygen had to be devised

in order that protoplasm could manifest itself in great, complex organizations. The human lungs have a surface area of about 80 sq.m. To visualize this, imagine a tissue, 0.0003 mm. in thickness, and measuring roughly 9 m. (30 ft.) on each side. Such a sheet is more than ample to assure the intake of oxygen and the excretion of carbon dioxide by diffusion. It may puzzle the reader to know how the equivalent of a 30-ft. square sheet of alveolar tissue can be packed into the body. The feat is accomplished by dividing it into microscopic alveoli which present an enormous respiratory surface in comparison with their mass. In the course of the evolution of breathing membranes, there has been a transition from respiratory laminae, or sheets, to undulating membranes offering relatively greater surface area, to microscopic hollow respiratory spheres, offering the greatest relative surface area. In connection with the great respiratory surface, it must be remembered that this is only part of the picture, for an equivalent red blood cell surface area is requisite to give the mechanism meaning. In anemia with loss of red blood cells or in cases of serious malaria, which may involve great loss of red blood cells, or in carbon monoxide poisoning, which makes it impossible for the red blood cells to function, death actually results by asphyxiation because one of the partners active in respiration has been eliminated.

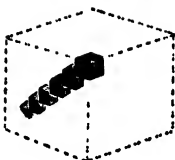
It is instructive to examine further this relationship of surface area to mass or volume, since the body has taken advantage of this changing relationship, not only with respiratory tissue, but with blood cells and digestive and excretory tissue; in fact, the very division of cells into microscopic unit offers a wide surface for a given mass or volume.

Weiser points out that a cube 1 cm. on each edge has a surface of 6 sq. cm., or 0.93 sq.in. (Fig. 188). If this is subdivided into particles $\frac{1}{1,000}$ micron long at each edge, these particles present a surface of 6,000 sq.m., or 7,176.0 sq.yd., or approximately 6/7 acre. The microscopic alveoli of the lungs, while presenting only 80 to 90 sq.m. of surface, nevertheless make possible the almost instant diffusion of gases through their lining membrane. The fish and perennibranch amphibian offer a much smaller gill surface to the water, and the turtle or alligator with the reticular arrangement of the lining membrane in the sac-like lungs also is far behind the mammal in lung area. Besides this, gill breathers suffer the disadvantage of living in a medium with 1 per cent of available oxygen, compared with 20 per cent available to lung breathers. Such facts enable us to deduce in part the limits of performance of various animals. These limits are determined among other variables by the actual physicochemical constitution, *i.e.*, relative amount of respiratory

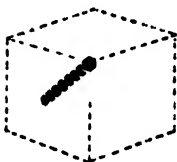
tissue, numbers of red blood cells, heart rate, etc. The scale of performance, of achievement, of being is in the last analysis dependent upon oxygen capacity, upon red blood cell count, upon number of cortical cells plus their ability to secure all the oxygen they require on demand, as well as upon the excretion of carbon dioxide.



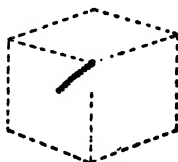
A Volume = 1 cc.
1 cm. = length of each edge
Surface area = 6 sq. cm.



B Volume = 1 cc.
1 mm. = length of each edge
Surface area = 60 sq. cm.



C Volume = 1 cc.
0.01 mm. = length of each edge
Surface area = 6,000 sq. cm.



D Volume = 1 cc.
0.001 mm. = length of each edge
Surface area = 6,000 sq. m.

FIG. 188. Diagram to show the relative increase of surface by reduction of the size of the object. By decreasing the size of the air pockets, or alveoli, of the lungs the surface area may be greatly increased. In man it comprises about 80 sq. m.

COMPARATIVE ANATOMY

Amphioxus. Amphioxus has peculiar gills. They represent an open, gelatinous, supporting *grillwork* extending along the cephalic half of the body in the wall of the pharynx. The grill is made up of *primary* and *secondary arches*, with short cross pieces, the *synapticula*. The primary

and secondary arches are lined with a single layer of *ciliated epithelium* in which are numerous mucous cells. The presence of these *mucous cells* is understandable, since the pharynx is a specialized division of the foregut and as such is part of the digestive system. Since the food of *Amphioxus* is of minute particles, the secreted mucus captures such bits and the cilia move them caudally. Such movement of food is not haphazard but is concentrated largely in two specialized grooves, one at the top and the other at the bottom of the pharynx, the *epibranchial* and the *hypobranchial grooves*, respectively.

The blood vessels which traverse the epithelial layer are branches of the *contractile ventral aorta* and originate from *bulbilli*. The vessels form *afferent branchial channels*, and after traversing the gills they continue as *efferent branchial arteries* which unite into *paired dorsal aortae*. The *bulbilli* are contractile enlargements of the afferent vessels. The further course of the circulation is described in connection with the account of the vascular system.

Water taken in by mouth escapes from the pharynx into the atrial cavity, between the pharynx and the body wall. This space is actually a peribranchial chamber outside the true body cavity. It communicates with the outside by the *atriopore*, situated on the midventral line, anterior to the anus.

While the respiratory system of *Amphioxus* is not typical of the vertebrate pattern, the essentials of a true vertebrate respiratory system are nevertheless present. These are a thin, ciliated epithelial sheet, permeable to oxygen and carbon dioxide; a capillary network carrying blood to and from this sheet; rods which support this epithelium under various stresses.

Cyclostomes. Cyclostomes have a variable number of gills (Fig. 189). *Bdellostoma* has 6 to 14 pairs; *Petromyzon* has 7. They show a departure from the typical arrangement, since they occur in pouches and communicate with the pharynx by internal and with the exterior by external pores. In *Petromyzon* the gills open internally into a branchial duct that lies ventral to the pharynx and opens into the latter. Externally they open by 7 pairs of pores. In the remaining cyclostomes the gill pouches communicate with the outside and into the pharynx by branchial canals.

It will be recalled that the cyclostomes are external parasites, attaching themselves by the cone-shaped, suctorial mouth to their victims. This raises the question as to how the gills operate. In *Amphioxus* and fishes, water is taken in by mouth and expelled through the gill slits. In cyclostomes apparently it is not only taken in but also expelled

through the external gill openings, at least when the mouth is attached to a victim.

The gills are arranged in lamellae separated by connective tissue and interbranchial septa. The epithelial membrane is pleated, offering greater surface for exchange of gases. Each leaf in the fold receives an afferent vessel, and together these vessels anastomose in a rich capillary

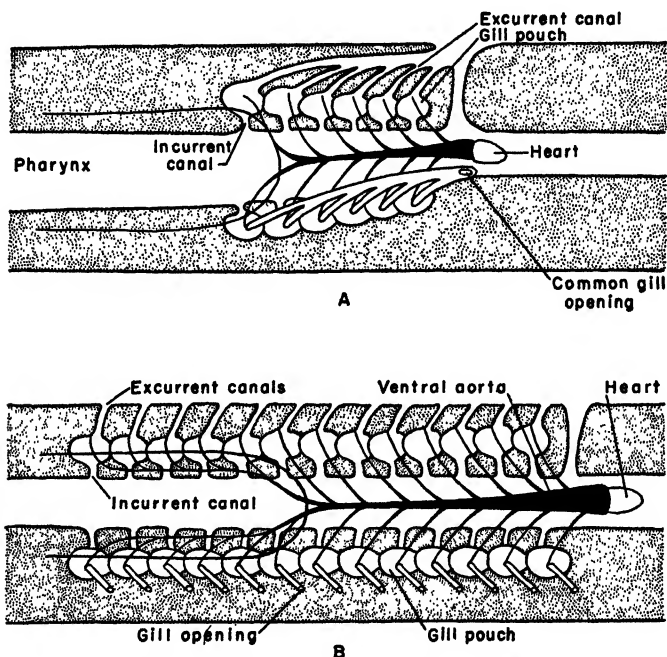


FIG. 189. The pharynx and gullet of the cyclostome. A, *Myxine*. Water passes from the pharynx via incurrent canals to the gill pouches. It leaves the pouches by excurrent canals and a common gill opening B, *Bdellostoma*. Water enters the pouches as in A but leaves the gills by multiple excurrent ducts. (After *Kükenthal*.)

plexus. The blood source to the gills is the paired truncus arteriosus, which extends forward ventral to the pharynx and gives off afferent vessels which ascend in the gills. Efferent vessels unite dorsally in a dorsal aorta which distributes oxygenated blood to the body as it does in the fishes.

Fishes. The primitive number of paired branchial arches in fishes is seven. Modifications in the first and second pair to form jaws and

hyoid arch supports leaves five pairs of functional gill arches as the most usual number. As in the Acrania, gills are evaginations from the pharynx met by invaginations of the adjacent external skin. The break-through at the junction of invagination and evagination becomes the external gill opening, or gill slit. Pharyngeal pockets are formed between the slits and the supports. The branchial pouches so formed are separated from each other by supporting cartilaginous or bony gill

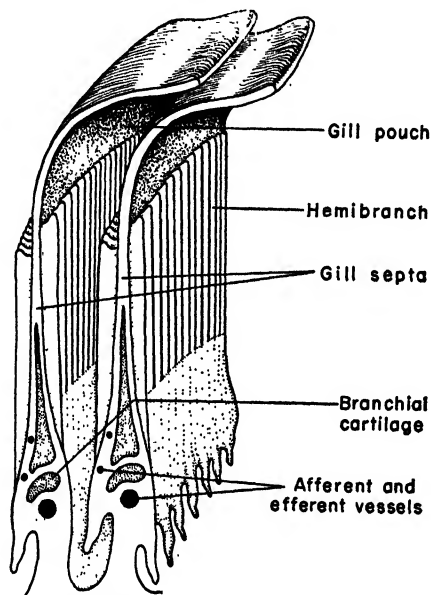


FIG. 190. The elasmobranch gill. The functional gills are separated by septa; one-half of a gill, or hemibranch, is attached to each side of the membrane. The spaces between opposite hemibranchs are the gill pouches. Blood enters and leaves the gills by afferent and efferent branchial arteries, respectively, at the base of each gill.

bars covered with connective-tissue septa (Fig. 190). In cartilaginous fishes, these septa attach to the undersurface of the skin and become lined with specialized breathing epithelium, the true gills. In many of the bony fishes the septa do not attach to the skin, and the gills are free at these peripheral margins. The epithelium of the gill, of probable endodermal origin, is arranged as a hemibranch on each side of a branchial pouch. The two hemibranchs on opposite sides of the same interbranchial septum constitute a holobranch. Gill rakers, small, finger-like

extensions of cartilage or connective tissue, frequently extend from the convex sides of the gill arches. They prevent food or debris from passing from the pharynx into the pouches.

Blood Supply. An elasmobranch gill includes a cartilaginous arch with its connective-tissue covering, a respiratory epithelium, and nerve and blood supply. The latter, as in cyclostomes, is passed to the gills by afferent branchial arteries. These direct branches of the ventral aorta are described more fully in Chap. 10, The Circulatory System. The first and third main branches on each side are subdivided, resulting in five afferent vessels to each side, one to each functional gill. Ascending along the cartilaginous arch, they send small, regularly placed twigs into the respiratory tissue. Capillary anastomoses pass the blood into efferent trunks which carry oxygenated blood into the dorsal aorta. In the common dogfish, four radices aortae on each side guide this blood into the main trunk of the dorsal aorta.

The ninth and tenth cranial nerves supply the gills. The ninth passes dorsal to the second branchial pouch and gives off a pretrematic, a post-trematic, and a pharyngeal branch to the gill pouch and to the branchial muscles of the third arch. The pretrematic branch is sensory, the post-trematic mixed; its motor fibers supply adjacent branchial muscles, while the pharyngeal branch is sensory to the pharynx and mouth. The tenth cranial nerve has a similar pre- and posttrematic and pharyngeal distribution to the remaining gills. The jaw, a modified gill arch, and the hyoid arch, no longer directly associated with respiration, are supplied by the fifth and seventh cranial nerves, respectively.

In bony fishes the functional gills are usually reduced to four pairs; loss of the outer attachment of the interbranchial septum causes the branchial pouches to disappear. A bony operculum, or covering, attached to the hyomandibular arch, not only protects the otherwise exposed gills but by its movements permits water to circulate more freely around them.

The gill slit between the hyoid and the first functional gill arch, known as the spiracle, has a vestigial gill attached in the elasmobranchs and in a few bony fishes. In most of the latter, however, while it may appear embryonically, it is lost in the adult. External gills may appear in some elasmobranchs as well as in bony fishes. These are not retained. The hyoid arch as well as the inner surface of the operculum may also be supplied with gills.

Accessory gills, in some fishes, adapt them to stagnant, slimy waters [e.g., *Charias* and the climbing fish (*Arabas scandens*) of Indiá]. According to Ihle, the latter prefer land to water life. Their poorly developed

gills play a secondary role to the accessory gill, which covers a labyrinthine bony lamella associated with the first branchial bar.

Ihle points to the fundamental similarity of gill and lung breathing, as exemplified in those fish in which gills take a secondary role as breathing organs. Thus, in *Amphipnous* of East India, gills are restricted to the second gill arch, while the wall of the first gill clefts evaginate caudally into paired pouches, although these are not true lungs. Such examples support the view that gills and lungs belong structurally to the same system.

Other modifications of the respiratory organ and respiratory function appear in the gut breathing of some of the bony fishes (*Cyprinidae* and *Siluridae*) in which specific areas of the intestine are highly vascularized and the air taken into the intestine may be expelled through anus, mouth, or gill slits.

Branchial Muscles. The branchial muscles beginning with *Amphioxus* are derived from the muscular layer of the intestinal wall, which in turn is derived from the lateral plates of the embryo. Thus they originate from the hypomere rather than from the myotome. In *Amphioxus* they retain their smooth character. In the cyclostomes they are striated and act as gill constrictors, since their arrangement around the gill pouches and underneath the somatic muscles permits such action. In the remaining vertebrates the branchial muscles have found their way to the surface and displace the epibranchial and hypobranchial somatic muscles. Eventually they lie subcutaneously. In addition to the muscles with purely branchial functions, the muscles of mastication and of the hyoid apparatus are of visceral derivation.

The visceral muscles extend from the first gill cleft to the shoulder girdle. They include a superficial constrictor from which interbranchial muscle fibers pass medially to the interbranchial septa. This superficial constrictor sheet originates from the occipital region and the dorsal fascia and inserts on the gill bars and below the gills in another superficial fascia. The sheet is interrupted by the gill slits, and its action closes them. Further differentiations account for a group of short adductors on the medial sides of the branchial bars and interarcual muscles which connect the upper segments of visceral arches with each other or with adjacent bars. The gill muscles are innervated as indicated by the ninth and tenth cranial nerves, those of the jaws by the fifth, those of the hyoid arch by the seventh.

Dipnoan Gills. The dipnoan fishes occupy a peculiar position in the piscian class, since in a sense they bridge the gap between water and air breathing. This does not imply that they are ancestral to land forms,

since evidence today indicates that the crossopterygians, also air breathers, were the likely ancestors. Gills and air bladders are present in the Dipnoi, but not equally developed in all genera. *Neoceratodus*, classified as a monopneumonian (single lung), has four pairs of functional gills, a vestigial hemibranch associated with the hyoid cartilage, and a

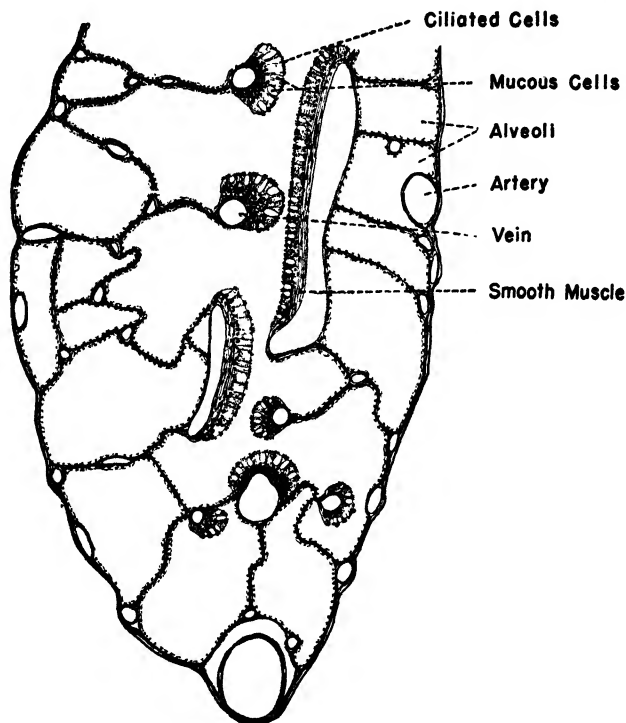


FIG. 191. The amphibian lung. The amphibian lung is a sac-like structure with an epithelial-vascular network internally. Mucus-secreting and ciliated cells constitute the membranous lining. Blood vessels course through this network.

single air bladder or lung. The latter, dorsal to the digestive tract, joins the tract by a pneumatic duct. In *Protopterus* and *Lepidosiren*, classified as dipneumonians (two lungs), the last three gill pairs are functional, while the first two arches do not carry respiratory tissue. A pair of air sacs occur as dorsal outgrowths of the alimentary canal. The spiracle has disappeared in both the monopneumonians and the dipneumonians. An interesting accessory breathing organ is developed in the male *Lepido-*

siren. The animal guards the eggs at the river bottom and is unable or unwilling to come to the surface to swallow air during the period of egg development. Delicate, highly vascularized filaments grow from the pelvic fins at this time, serving apparently as accessory breathing organs.

Amphibia. The Amphibia recapitulate certain steps of gill evolution as these steps appeared in the fishes. Embryonic gills, numbering 3 to 5 pairs, are always present. Besides these internal gills, external ones develop in the urodeles and the Anura, to disappear later in many genera. In a few such as *Amphiuma*, *Necturus*, and *Proteus*, they are retained. An opercular fold beginning at the hyoid arch closes over these external gills in the Anura and in the lung-breathing urodeles, and the external gills are absorbed. Anura have simple lungs without a true trachea (Fig. 191); in urodeles the beginning of a laryngotracheal sac occurs. In aglossal amphibians the distal part of the trachea is divided, marking the first appearance of bronchi.

Amphibia, in the absence of ribs, diaphragm, and specialized breathing muscles, swallow air; contraction of abdominal muscles causes its expiration.

LUNGS

The question of the origin of the lungs has interested and confused biologists for many years. Today it is generally accepted that the swim bladder and the lungs are homologous organs. Both are derived from the pharyngeal wall; both first appear as air-filled vesicles. The air bladder, originally an accessory breathing organ, in the land form developed a specialized pharyngeal opening (larynx) and ducts (trachea and bronchi), while its musculature was derived from branchial muscles.

The Dipnoi and crossopterygians bridge the gap between land life and water life; at least they point the way in which this gap has been bridged. A variable gill development has been pointed out in *Neoceratodus* with a single lung sac, compared with *Protopterus* and *Lepidosiren* with two. None of these genera are divorced from aquatic life, save in a very restricted sense; at best the two-lunged forms build a mud cocoon about themselves when conditions are not propitious for aquatic life and await return of the water, in a quiescent, protected state, during which the lungs supply sufficient air to maintain life.

It should be emphasized that lungs and gills exist simultaneously only in the Dipnoi. Both arise as pharyngeal evaginations. In Dipnoi the lungs are sac-like; in *Neoceratodus* the single lung is partially divided by a connective-tissue wall. The respiratory surface is greatly increased, in both mono- and dipneumonians, by alveoli. In both groups, too, the

blood supply is copious. The arterial blood to the lungs is furnished by the pulmonary artery, a branch of the sixth aortic arch in *Neoceratodus* and *Lepidosiren*, and by independent branches of the dorsal aorta in *Protopterus*. It will be recalled that these arterial vessels to the lungs carry reduced blood.

Amphibia. Amphibian lungs are bilobed epithelial sacs associated with the floor of the pharynx by a narrow opening, the glottis (Fig. 191). A tube of variable length and development unites the lungs with the pharyngeal cavity. Cartilage, significant for its supporting value, becomes associated with the glottis as well as with the trachea. It serves the further purpose of preventing collapse of the breathing tube. The inner surface of the sac-like lungs is increased by folding of the epithelial lining and by the increase in vascularization supported by additional connective tissue in the lung wall.

Respiration is carried on by swallowing the air while the nares are closed; expulsion is brought about by contractions of the abdominal muscles. Smooth muscles in the lung wall partly compress the air-filled lung and assure ventilation in its several alveoli.

Laryngeal and Tracheal Cartilages. As indicated, cartilages supporting the larynx and trachea appear in Amphibia. The opening into the larynx is a narrow, elongate slit, the *aditus laryngis*, or *glottis*. A trachea as such is not indicated in the Anura, since the glottis opens almost immediately into the lungs; it is better developed in the urodeles, correlated with appearance of the neck. The cartilages supporting the larynx and trachea are derived from the posterior branchial cartilages. Below the hyoid body these are differentiated into paired *arytenoid cartilages*, supporting the membranes around the glottis, and into *cricoid elements* at the head of the trachea. The last may fuse with tracheal fragments in the tracheal wall. With the appearance of a definite trachea, additional cartilaginous elements from the *cricotracheal cartilage* distribute themselves in its wall. The laryngeal mechanism is controlled by paired *dilator* and *constrictor muscles* that regulate the opening and closing of the glottis.

Because of the central significance of the laryngeal apparatus, whose further evolution resulted in speech and vocal communication, a description of the vertebrate larynx appears warranted. The effects of this metamorphosis far transcended its origin from mucous membrane, cartilage, muscle, and nerve, for it becomes the mechanism for speech.

A sagittal section through the larynx and trachea reveals the rim of the glottis, lined with mucous membrane. The rim marks the opening into the *vestibule* of the larynx. This small chamber is limited below by

the *vocal cords*. The cords are a superior and inferior pair separated by a longitudinal sulcus.

The lower pair are the true vocal cords. The expansion of the region below the cords is the *pulmonary vestibule*, in contrast to the laryngeal vestibule, which lies above it. The cords are of elastic tissue and terminate in cartilaginous extensions. The *cricoid* is a small cartilage at the level of the lung opening below the pulmonary vestibule. Sound is produced by closure of nostrils and mouth, followed by contraction of abdominal muscles, which push air into the mouth cavity; depression of the larynx increases the volume of the mouth cavity. The momentary opening of the nares permits the air to rush out. This is succeeded by quick inhalation of air and a repetition of the steps indicated. Continued air expulsion sets the cords into vibration. The voice of the female is weak; that of the male is strengthened by a pair of resonators, the vocal sacs, which when active become greatly expanded in the floor of the mouth.

Amniotes. In amniote animals, gills are transient embryonic structures which are never functional as breathing organs. They are epithelial-lined branchial pouches and branchial bars, whose subsequent fate is dealt with in detail elsewhere (page 474). Suffice it to state here that the skeletal elements form the jaws, the hyoid apparatus, the larynx and the trachea, and the ear ossicles, while the epithelial lining of the floor, in part, and of the pouches is transformed into thyroid and parathyroid glands, thymus, and ultimobranchial bodies. Lungs have entirely replaced gills in the amniotes. The amnion itself is a protective structure which apparently reduced the hazards of development. Instead of a roving larval existence, such as the fish and frogs experience, the amniote remains relatively stationary within the protective custody of the amnion and related structures. In reptiles and birds this most interesting life chapter evolves in the confines of the eggshell; in mammals, with the exception of the monotremes, it evolves within the uterus. With the completion of this highly charged story, the young animal is ready to lead its own quasi-independent existence, although tied to the parent by close temporary bonds in the birds and by increasingly essential ties in mammals.

Reptiles. Reptilian lungs are a transition between the sac-like lungs of Amphibia and the more highly alveolar and vascular types of birds and mammals. Among the reptiles the simplest lung type is in the lizard, where a single short trachea bifurcates into two lung sacs. In turtles, snakes, and Crocodilia, a great number of alveolar pockets, with extra- and intrapulmonary bronchi, bring about a further division of the latter

into primary, secondary, and even tertiary bronchi. Appearing also are cartilages in the walls of the primary bronchi. Addition of alveoli, through reduction of the single lung sac into many compartments, increases the respiratory surface. In snakes, with the great elongation and streamlining of the body, the lungs, like the liver and kidney, are reduced to single elongate organs.

The mechanism for introducing air into the lungs has evolved beyond the simple swallowing stage to the level of the utilization of body and rib

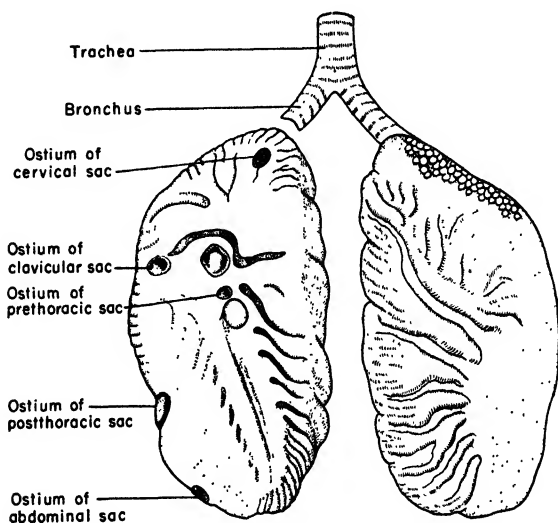


FIG. 192A. The bird lung (ventral view). The paired avian lungs are unique in that air passes completely through the lungs into air chambers. This makes for more complete ventilation of the respiratory chambers. (After Stressemann.)

muscles for expansion of the trunk cavity. This causes air to be drawn in, and subsequent contraction of intercostal and abdominal muscles forces its expulsion. These muscular activities in reptiles are still supplemented by active swallowing movements, as in the Amphibia. The heavily armored turtles apparently rely largely on swallowing movements to capture air.

The reptilian larynx has a single large cricoid cartilage supporting a pair of small arytenoids above it. In the Crocodilia the larynx, in addition to paired arytenoid cartilages, has a thyroid plate and a cricoid ring. An epiglottis is lacking. The trachea may be of considerable

length, which in the Crocodilia is further increased by coiling. In contrast to this loop formation, which may add as much as 18 in. to its length, the trachea of the alligator is a straight tube. The tracheal rings in this order are complete. True vocal cords are wanting, although these saurians produce sounds by mucous membrane folds in the larynx.

Birds. The lungs of birds are relatively small, a condition that might lead to the unwarranted assumption that they are less efficient, for example, than those of the mammals (Fig. 192). This is not the case, for their smallness is probably the result of their peculiar constitution, one of the key features of which is the association of sizable air chambers, or sacs, as accessories to the lungs. This permits a thorough ventilation of respiratory tissue, not only on the intake of air, when it traverses the lungs on its way to the sacs, but in its exhalation, when it passes from sac to lung to the exterior.

The following account of the bird lung is based largely on the excellent description of Erwin Stresemann. At the bifurcation of the *trachea*, the primary, or *dorsal*, *bronchus*, supported by *cartilaginous rings*, widens into the *vestibule* as it enters the medioventral aspect of the lungs. In the mediodorsal side of this tube, four to six openings lead into secondary *ventral endobronchi*. The primary bronchus narrows and continues caudally as the *mesobronchus*, into which open two rows of 7 to 10 *dorsal ectobronchi*. Between these two rows a series of smaller openings lead to the *parabronchi*, which are tertiary and of which the functions will be more fully described later (page 372).

The primary mesobronchus continues caudally and divides, one duct opening into a *postthoracic*, the other in the *abdominal sac*, both beyond the limits of the lungs. These sacs are inspiratory; the postthoracic extends into the space below the lungs and in some instances into the pelvic cavity; the abdominal occupies the lateral region of the body cavity and

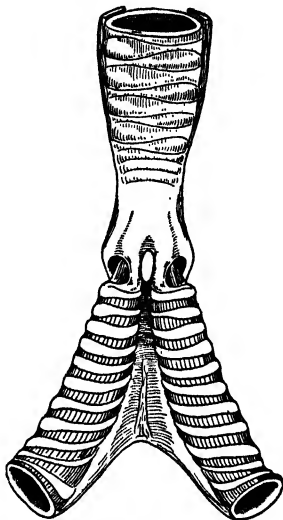


FIG. 192B. The bird syrinx (domestic goose). At the forking of the trachea a higher specialized sound-producing mechanism, the syrinx, has developed. This involves bronchial cartilages and membranes, and in some species has specialized muscles associated with it.

sends diverticula between the lumbar and sacral vertebrae and into the femur.

From the ventral endobronchi, three pairs of sacs extend anteriorly and laterally. These are: (1) the cervical sac, which passes anteriorly to the level of the third cervical vertebra and sends diverticula into the spinal canal; the latter diverticula may fuse with each other; (2) the clavicular sac, usually fused between the clavicles and surrounding the lower end of the trachea and syrinx; they send diverticula into the shoulder region and into the sternum, coracoid, clavicle, and humerus; (3) the prethoracic sac, occupying the space around the pericardial cavity, and the esophagus; these sacs are expiratory in function.

The air sacs are extremely thin, with few nerves and blood vessels. They have an inner layer of squamous epithelium and supporting connective tissue, continuous with the lining of the bronchi, and an outer serosal layer. Their arteries are direct branches of the aorta, and their veins open into the vena cava.

Air passes directly into the dorsal bronchi and thence into the abdominal and postthoracic sacs. It is returned from these sacs by recurrent canals (saccobronchi) to the basal parts of the dorsal bronchi. The latter are a highly branched system of canals leading eventually into small tertiary parabronchi. These extend over the medial and caudal borders of the lungs and open eventually into the system of ventral bronchi which communicate with the vestibule. The parabronchi are the site of gaseous exchange. By repeated divisions they give rise to small bronchioles, or air capillaries, which anastomose widely into a fine network of which the meshes are taken up by a similar network of blood capillaries.

The bird lung is a tubular system in which the dorsal bronchi permit the air to enter and the ventral bronchi permit its egress, in contrast to the alveolar system of mammals. Both afferent and efferent tubes are supplied with air sacs that may be closed by valves or by smooth muscle contractions.

Enlargement of the space about the three anterior sacs pulls air from the postthoracic and abdominal sacs by way of the recurrent and parabronchial tubes. If the front sacs are compressed, air is pushed into the vestibule and to the outside, provided that the valves of the posterior sacs are closed. If the air from the posterior sacs is not exhaled, it may be recirculated into the posterior sacs. This, according to Stresemann, explains the ability of certain diving ducks to remain under water for as long as 15 min. without injury and may account for the slow respiratory rate in many birds, *e.g.*, 4 per minute for the pelican, 6 for the vulture,

13.5 for the turkey cock, 18.5 for the common fowl, and 25.5 for the pigeon.

The bird larynx is a ventral thyrocricoid plate, incomplete dorsally, and partially surrounded by paired arytenoid cartilages guarding the laryngeal opening. The arytenoids have a small cricoid cartilage wedged between their dorsal margins. The tracheal ring cartilages are complete in some birds and incomplete in others, where they may overlap dorsally, the dorsal ends held together by elastic connective tissue. Ossification of tracheal rings is widespread, outside the nonflying ratites. The trachea usually descends to the right of the cervical vertebrae and forks on its entrance into the thorax. In a *Cygnus*, *Anser*, *Gallus*, bird of paradise, and some others, the trachea may execute a loop between the arms of the furcula before entering the thorax. In some species only the males exhibit this loop.

The bronchial rings are not complete in most birds, and the most proximal are frequently modified by the development of a syrinx (Fig. 192*B*). The syrinx, and not the larynx, is the sound-producing chamber of birds. It is best developed in the songsters. The following account, again based in part on Stresemann's, describes this mechanism in the passerine order Oscines, comprising over 5,000 species of singing birds. In these the last 3 to 6 tracheal rings are complete and become fused to form the drum. This may be cartilaginous or ossified. The distal margin of the drum rests on the bifurcation constituting the first bronchial cartilages. The first three of the latter on either side are heavier, broader, and less elastic than the lower. They are known as the syringeal arches. The dorsal part of the first of these arches, furthermore, fails to ossify in many species and becomes the dorsal tensor cartilage to support the membrane of the syrinx. A second supporting cartilage from the ventral end of the second bronchial arch also supports this membrane ventrally. At the medial junction of these two bronchial arches, the bony pesselus juts into the lumen of the trachea. This is a plate, covered by an elastic connective tissue, and has at its base the elastic internal vocal membrane. Caudally this tympaniform membrane continues as the covering for the medial wall of each primary bronchus; the bronchial rings are incomplete and absent from this medial portion of the bronchial wall. The membranes of the two sides are further connected by an interbronchial membrane, the bronchiodesmus. In the space between pesselus and this membrane is an extension of the clavicular air sac, associated with the lungs.

A second membrane, or external tympaniform membrane, lies in the lateral wall of the bronchi.

The musculature acting on the syrinx varies greatly. In birds like the ostrich and the common fowl it is entirely absent; in some birds of prey a pair of muscles extends from the trachea to the bronchi. In many Oscines, three to nine pairs of syringeal muscles govern the actions of the syrinx. These muscles, in the production of sound, act in part on the membranous chords of the syrinx; others may produce a closer approximation of the lowest tracheal and the upper bronchial rings. The musculature is innervated by the tenth and twelfth cranial nerves.

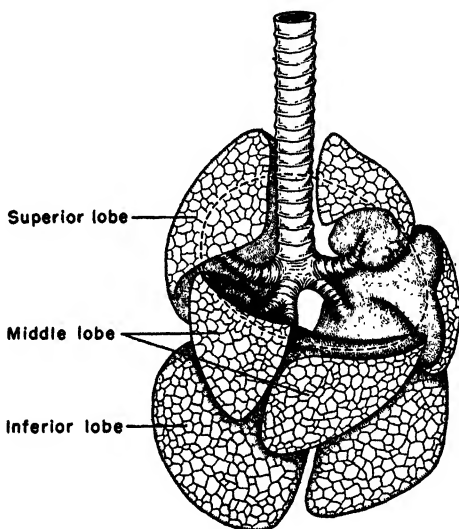


FIG. 193A. The dog lung. The right lung consists of three major lobes; the left of two. Note the space for the heart. The primary bronchi begin at the forking of the trachea.

Mammals. Mammalian lungs are more closely related to reptilian than to avian lungs (Fig. 193A, B). In comparison to the reptilian, they have undergone an enormous increase in alveoli, in bronchi, in vascularization, in specialization of the larynx, and in perfection of a bellows system, which is aided by the ribs, intercostal muscles, and diaphragm. Further refinements relate particularly to the arrangement of alveoli on the terminal bronchioles in comparison with alveolar pockets budded off from the various orders of bronchi in the reptiles. The number of alveoli may reach 3 million to 4 million in man in comparison with several thousand, at most, in reptiles. It is perhaps most satisfactory to visualize the mammalian lungs as built around the two

primary bronchi, which by dichotomous divisions give rise to bronchi of various orders, followed by bronchioles of extremely small caliber. The pattern of the air tubes and their terminations appears tree-like, while the epithelium, blood vessels, connective tissue, and smooth musculature obscure the branches and the twigs of the tree.

The bronchial skeletal system is cartilaginous, and its development differs widely in various groups. In the Primates the bronchial cartilages are not prominent and are absent entirely, according to Ihle, in the

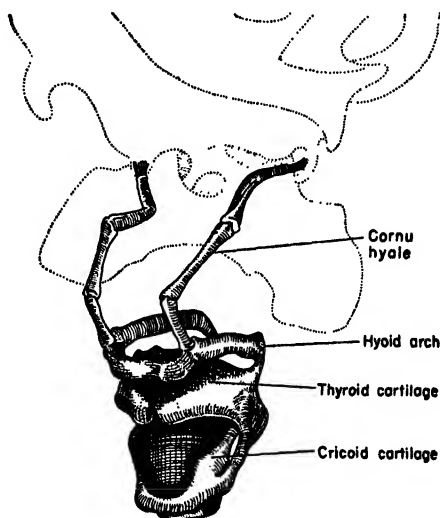


FIG. 193B. The dog larynx and its relation to the hyoid arch. The hyoid arch effectively unites the laryngeal apparatus with the stylomastoid process of the skull. In the horse, the superior cornu of the hyoid articulates directly with the stylohyoid process. In man an elongate stylohyoid ligament replaces the bone.

South American howling monkey *Mycetes*. In others like the marsupials and rodents it is poorly developed. The lungs are attached to the body chiefly about the hilus, at the original bifurcation of the bronchi in close proximity to the points of entrance and emergence of the blood supply. Additional support is offered along their dorsal margins by pulmonary mesenteries which attach to the dorsal body wall and by the extensions of the pleural sacs which surround the lungs and line the thoracic cavity.

The lungs are invested by a serous membrane, the *pleura*, which not only lines the thoracic cavity but which is reflected over the lobes of the

lungs and their fissures. That portion which lines the thorax and covers the diaphragm is the parietal pleura; the reflected layer over the lungs is the pulmonary. The serous secretion from this epithelium is a lubricant during respiration and prevents friction and adhesions between lungs and thorax.

Posteriorly the reflected pleurae of the two sides enclose a narrow space, the *posterior mediastinum*. An extension of this posterior sheet is the *pulmonary ligament*, one on each side attaching the posterior margin of the lung to the thoracic wall. Anteriorly the pulmonary pleura follows the contours of the lungs and is reflected over the pericardium as the *pericardial pleura* from the sternum to the vertebral column. The region thus enclosed is called *superior mediastinum* above the pericardial level and *inferior mediastinum* from the pericardium down. The latter is divided further into the *anterior mediastinum*, the region in front of the pericardium; the *middle mediastinum*, which contains the pericardium and its contents; and the *posterior mediastinum*, the area behind the pericardium.

The lung tissue itself is highly elastic. When removed from the body it returns to its original shape after compression. When sectioned it has a spongy appearance; bronchi and bronchioles of various sizes as well as blood vessels are revealed, in addition to the spongy tissue. The upper end of the lung is its *apex*; the lower where it rests on the diaphragm is the *base*. Since its shape is determined by that of the thorax and heart, its contours follow faithfully the anterior, posterior, and inferior borders of the thorax. Medially each lobe has a cardiac impression, greater on the left side, as well as grooves for the esophagus, subclavian artery, superior vena cava, and azygos vein on the right side; for the aortic arch, subclavian artery, and left innominate vein on the left side.

The human left lung is divided into two lobes by a deep interlobar fissure; the right lung into three by two fissures. In the cat, rabbit, dog, and horse each lung is subdivided into three lobes. The bronchi continue to divide dichotomously until they end in the lobular bronchioles. The larger bronchi have an outer fibrous connective tissue covering the cartilaginous supports, followed by irregularly arranged circular bands of smooth muscle fibers immediately over the cartilages, while the internal lining is a ciliated mucous membrane. The smallest *bronchioles* subdivide into *respiratory bronchioles*, which continue as *alveolar ducts*. These are expanded into *alveolar sacs* in their first portion and terminate in a variable number of *alveoli*, the final air sacs. The latter are vesicles of simple squamous epithelium closely surrounded by a capillary network, the chief site of external respiration.

In addition to the blood supply from the *pulmonary arteries*, which

send unaerated blood to the lungs for oxygenation, the lungs receive *bronchial branches* from the aorta, which supply nutrition to the lung substance. The *pulmonary veins*, which return pure blood to the left atrium of the heart, represent fusions of smaller vessels originating ultimately in the capillary network. The larger vessels follow the bronchi in their ramifications through the lungs.

The bronchial veins return some of the blood contributed by the bronchial arteries to the heart via the *azygos vein*; the bulk of the bronchial blood, however, is returned by the pulmonary veins.

Innervation of the pulmonary mechanism is by the autonomic nervous system, which forms *bronchial plexuses* at the root of the lungs and from which nerve filaments follow the bronchi to supply efferent fibers to the smooth muscles and to the mucous membrane.

Asthma, which is a spasmodic contraction of this smooth musculature, closing or partly occluding the respiratory bronchioles and thus depriving the alveoli of air, may be relieved by proper dosages of adrenalin, which causes a relaxation of the smooth muscles and apparently a cessation of the secretion of the mucous membrane.

MAMMALIAN LARYNX

The laryngeal apparatus is more highly differentiated in mammals than in any other class. By this we refer particularly to its evolution as a sound-producing organ which has resulted in a mechanism producing not only squeaks, grunts, creaks, whistles, and melodious notes but speech. The latter involves much more than the emission of sound vibrations by a larynx or syrinx, since it requires a certain conformation of tongue, mandible, and hard palate, correlated with proper nervous activity. Further, use of sounds and systems of real communication imply an awareness or intelligence capable of giving them meaning.

Undoubtedly one of the great forces in making *Homo sapiens* human has been his cerebral-laryngeal-maxillary-mandibular-glossal apparatus, by which he could form words and give meaning and content to these oral symbols for ideas. This happy, coordinated evolution of several parts produced a mechanism that far transcended its origins. Certainly no one, making the most minute and detailed examination of the amphibian trachea, arytenoid-cricoid cartilages, and glottis would on that evidence alone have predicted the human voice, speech, oral communication, and the life of ideas and of reason.

Examination of the several parts of the human larynx, again in the absence of knowledge as to what it can render in creating speech, would not enable one to foretell speech and its implications from a dissection alone.

In primitive mammals, such as the duck-billed platypus, arytenoid, cricoid, and thyroid cartilages occur as separate plates fused only in the midventral line. The hyoid arch in close relation to the upper portions of the larynx is tied by ligamentous bands to the upper and anterior margins of the thyroid cartilages. The tracheal rings are incomplete, as they are in most mammals save the rodents, seals, some marsupials, and the lemurs. The epiglottis, a cartilaginous leaf supported by connective tissue and covered with mucous membrane at the entrance to the larynx, is a device developed in relation to the peculiar laryngeal-esophageal relations of reptiles and mammals particularly. The epiglottis is a lid which may be closed over the head of the larynx by reflex nerve action in the act of swallowing. It represents an *in situ* sesamoid development and is not a branchial arch derivative.

In the true mammals, the *thyroid cartilages* are fused into a shield-like plate, giving the structure its name, thyroid, meaning shield (Fig. 191). This shield is open dorsally, and associated with the inner surfaces of its lateral plates are the paired, ladle-shaped *arytenoid cartilages*. Arytenoid and thyroid plate are imposed on the single *cricoid cartilage*. Cricoid means ring-shaped and derives its name from its resemblance to a signet ring, whose band is wider dorsally than ventrally.

The following account is based on the dissection of the dog larynx with occasional references to other mammals. Only the broad outlines are followed, since space does not permit the minutely detailed description necessary for a comprehensive understanding of the mammalian larynx.

The supporting structures are unpaired thyroid, cricoid, and epiglottis cartilages, paired arytenoids, and corniculate and cuneiform cartilages (Fig. 194A, B). Closely associated but not an intrinsic part of the larynx, the hyoid bone attaches to the thyroid cartilage by the thyrohyoid membrane. Immediately below the cricoid cartilage the trachea proper, supported by some 16 C-shaped cartilages, descends into the thorax and forks into right and left primary bronchi.

The thyroid cartilage, largest of the supports, represents the fusion of two laminae, or plates, a fusion which includes only their anterior margins. A deep thyroid notch appears above this midventral fusion, while the prominence just below the notch is the so-called "Adam's apple," prominent in the human male. The laminae diverge posteriorly; their dorsal borders are extended as the superior horns, the ventral as the inferior horns. The upper join with the hyoid bone by the lateral thyrohyoid ligament; the lower articulate with the lateral margins of the cricoid cartilage.

An external line extending ventrodorsally in the dog and antero-posteriorly in the human larynx crosses the lateral lamina, dividing it

roughly into a smaller dorsal and a larger ventral area. The posterior area is covered by the inferior constrictor muscle of the pharynx, the anterior by the thyrohyoid muscles. To the line are attached, in addition to the above-named muscles, the sternothyroid muscles. To the anterior inner surface of the thyroid cartilage below the thyroid notch is

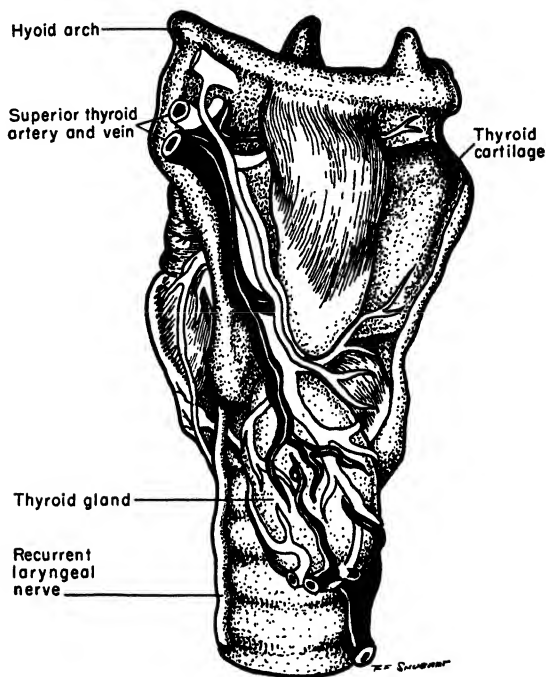


FIG. 194A. External view of human larynx.

attached the inferior end of the epiglottis by the thyroepiglottic ligament, the false and the true vocal cords, and the vocal ligament. To the margin of the thyroid notch and back to the greater horn is the attachment for the thyrohyoid and the lateral thyrohyoid membrane. The cricothyroid ligament at the junction of the lamina at the lower border of the thyroid unites it with the cricoid cartilage.

The cricoid cartilage is a complete ring with the broadest part of its band facing dorsally, while its ventral narrowed portion forms an arch. Its lateral laminae are seated inside those of the thyroid cartilage and articulate with the latter by articular facets. These articulations, sup-

ported by ligamentous capsules, are lined with synovial membranes. Anteriorly the arch is tied to the thyroid cartilage by the cricovocal membrane. Seated on the laminae of the cricoid cartilages and therefore adjacent to the inner surface of the laminae of the thyroid cartilage are the paired, pyramid-shaped arytenoids. The apices of these carti-

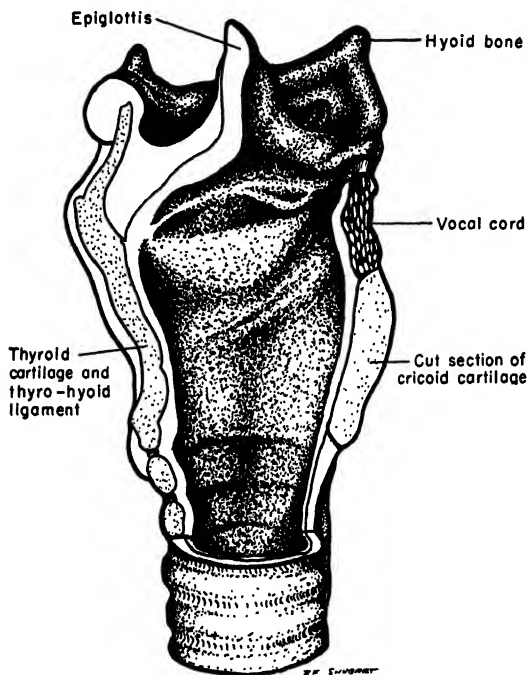


FIG. 194B. Midsagittal section of human larynx. The human larynx has transcended its original function as a gateway and trapdoor to the lungs by becoming the organ of speech.

laginous pyramids, directed posteriorly and medially, support the small corniculate cartilages. The vocal ligament is attached to small vocal processes extending from the base of these cartilages. Laterally and dorsally a pair of muscular processes give attachment to the cricoarytenoid muscles. As indicated, the arytenoids rest on the lamina of the cricoid cartilages, and at their approximated surfaces articular facets are developed.

TABLE 10. INTRINSIC MUSCLES OF THE LARYNX

Name of muscle	Origin	Insertion	Function	Innervation
Cricothyroid	Cricoid cartilage	Thyroid cartilage	Elevates and tilts back upper border of cricoid	Superior laryngeal nerve
Posterior cricoarytenoid	Posterior surface of cricoid cartilage	Muscular processes of arytenoid	Opens glottis	Recurrent laryngeal nerve
Lateral cricoarytenoid	Arch of cricoid cartilage	Muscular processes of arytenoid	Closes glottis	Recurrent laryngeal nerve
Oblique arytenoids	Base of one arytenoid to apex of other		Closes glottis	Recurrent laryngeal nerve
Transverse arytenoids	Between two arytenoids			
Thyroarytenoid	Medial surface of thyroid cartilage	Anterior border of arytenoid	Relaxes vocal folds and closes glottis	Recurrent laryngeal nerve
Vocalis	Medial surface of thyroid cartilage	Anterior border of arytenoid	Adjusts tension of vocal ligament	Recurrent laryngeal nerve
Thyroepiglottis	Medial surface of thyroid cartilage	Lateral margin of epiglottis	Depresses epiglottis	Recurrent laryngeal nerve

The remaining laryngeal cartilages are small corniculate nodules on the apices of the arytenoids, cuneiforms buried in the aryepiglottic folds, and the thin, perforated, tongue-shaped epiglottis attached below the thyroid notch on the inner surface of the thyroid cartilage and extending upward above the level of the hyoid bone.

The entire laryngeal cavity is lined with mucous membrane raised into

two parts of folds, forming the ventricular false vocal folds above and the true vocal folds below. The voice mechanism is operated by pulls on the arytenoid cartilages, which may tense the vocal cords, approximate their lips, or relax them.

The muscles producing these actions, as well as the modifications in the larynx associated with swallowing, are divided into extrinsic and intrinsic groups. The former, external to the larynx, tie it to adjacent structures. They include the hyoidean muscles, since these are functionally associated with the larynx. With the exception of the cricothyroid muscle, the intrinsic laryngeal muscles are associated with the inner margin of the thyroid cartilage.

Table 10, showing the attachments and functions of the intrinsic muscles in the human larynx, indicates a few of the adjustments necessary in speech formation and swallowing.

There is considerable sexual difference in the human larynx, as indicated by the following figures: The rima glottidis (opening between the vocal ligaments) has an average length of 23 mm. in the human male and 17 mm. in the human female. When stretched, this opening may be extended to 27.5 mm. in the male and 20 mm. in the female. The longer vocal cords of the male are associated with a lower pitched voice. Puberty brings about marked changes, particularly in the male voice. The larynx increases relatively in size, causing the deepening of the voice. Today this sex-limited feature is recognized as definitely associated with the increase in androgenic hormones secreted by the testis, probably under pituitary influence. Prepuberal castration results in the retention of a high-pitched voice.

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CHAPTER 10

THE CIRCULATORY SYSTEM

CHARACTERISTICS

The circulatory system is the result of the mountain's refusal to visit Mohammed. Many-celled animals, to exist at the high level to which the evolutionary forces, whatever their nature may be, have pushed them, require a mechanism for transport of oxygen, carbon dioxide, food, hormones, antibodies, etc. Such animal mechanisms function because they are built largely of semipermeable membranes and because the physical phenomena of diffusion, osmosis, and permeability are operative universally in protoplasmic structures. In single-celled and small-bodied animals the cells are in direct contact with food and oxygen through the aquatic environment. Since the animal cells of the complex Metazoa cannot come to the foodstuffs, the foodstuffs come to them and they arrive by way of the blood.

The success of the vascular system is due in part to the pressure which may be built up and maintained within it. This pressure is possible because innumerable anastomosing channels form a closed circuit, with the heart as part of the circuit, supplying the propelling force. Given the proper conditions, this assures adequate blood supply and continuous circulation to the remotest parts of the body.

The chordate heart and blood vessels, then, represent a closed system which has become adapted to various demands (Fig. 195). These demands include those of water, land, and air life; of cold-blooded and warm-blooded states; of herbivorous, carnivorous, and omnivorous food habits; of locomotor habits which vary from the extremes of the sluggish turtle to the agile lizard, the soaring man-of-war bird, and the racing greyhound.

The wide range in activity indicated above has not altered fundamental patterns in circulation. From *Amphioxus* to man it is retained as a closed system. From *Amphioxus* to man a part of the system pulsates, bulbilli on the ventral aorta in one case, and heart in the other. In all instances, gills, lungs, integument are the key centers in which one phase of the circulation is emphasized because of their close relation to the oxygen supply. The other phase is related to digestive tract and

organ systems that make available and use the energy released by the orderly cooperation of circulation and digestion. With changes in the respiratory mechanism from gill to lung or from gill to skin, circulatory changes are invariably correlated. It cannot be overemphasized that blood stands in a peculiar relation to gill, lung, kidney, liver, small intestines, and skeleton. Very properly these separate organs might be

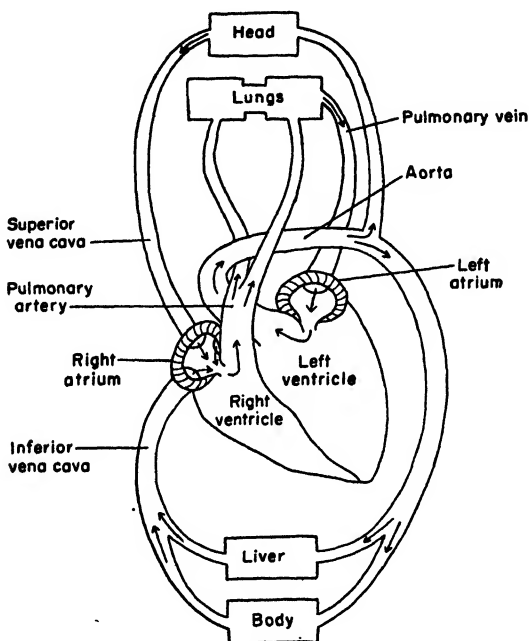


FIG. 195. The closed circulatory system. In such a system continuity is achieved between arteries and veins by a capillary network. Rapid circulation and considerable internal pressure are possible in such a system.

considered a part of the vascular system because of their dependence and functional association with the blood stream. This is in contrast with muscular and nervous systems, which are primarily blood users. This dependence led Frederic Ruysch (1638–1731), the Dutch anatomist, to the conclusion that “the tissues of the body were nothing but vascular networks variously arranged.” The ubiquitous nature of the blood channels interwoven in a dense vascular network throughout the body, which he revealed by injecting the vascular tree, led him to this conclusion.

A system so intimately tied to respiration, excretion, food, oxygen and carbon dioxide, transport, and energy release possesses characteristics that associate it with every other system of the body.

The fundamental structures by which the circulatory system is functionally associated with other systems is the capillary network. While larger channels, the arteries, lead the blood to muscle, gland, or nerve complex, the capillaries make possible the utilization of blood by these structures. In a sense, artery and vein are subsidiary to this capillary bed. The larger trunk lines are essential as carriers; the work of the blood for the benefit of the body becomes possible through capillaries. The nature of the formed elements in this liquid tissue will be discussed in another connection (page 422). For the present we shall concern ourselves with the tubes by which blood is sent to every portion of the body and to that remarkable pump, the heart, which keeps the stream in motion.

THE STRUCTURE OF THE BLOOD VESSELS AND THE HEART

The Artery. Vessels carrying blood from the heart to the body are designated as arteries. Beginning at the heart, the channels become smaller by continued branching, and when they reach calibers smaller than 0.3 mm., they are called arterioles. These are confluent with capillaries with lumina large enough to permit passage of red blood cells with diameters of approximately 7.5 microns. The arterial walls are three-layered (Fig. 196).

1. An inner layer, the tunica intima, with an endothelial lining of squamous cells, a single layer in thickness on the free surface, and an elastic network membrane variously developed, depending upon the size of the artery; this frequently appears folded or wrinkled in histological preparations;

2. The tunica media, an intermediate layer, mostly of circularly arranged smooth muscle fibers, and associated collagenous fibers except in very large arteries, where elastic connective tissue predominates;

3. The tunica adventitia, an external layer of connective tissue, largely directed longitudinally, collagenous and elastic in character, relatively thinner in larger arteries than in those of medium caliber.

In capillaries the endothelium persists. This, the only tissue common to the entire vascular tree, is developmentally the first layer and appears as a thin, homogenous membrane. Its cellular nature may be observed under silver nitrate staining, which reveals the flattened, nucleated endothelial cells. Pericapillary mesenchyme cells with presumably contractile qualities usually accompany the endothelial cells of the capillaries. It is at this level that oxygen and carbon dioxide exchange most fre-

quently takes place. At this site also the white phagocytic blood cells escape from the capillary by squeezing through the endothelium.

The capillary network anastomoses everywhere, leaving but little space in organs and tissues not traversed by this life-giving reticulum. In the resting state many capillaries are collapsed. According to Cajal, only approximately two-fifths of the capillary bed in a given area may be in operation when the body is at rest. When the need arises, the entire

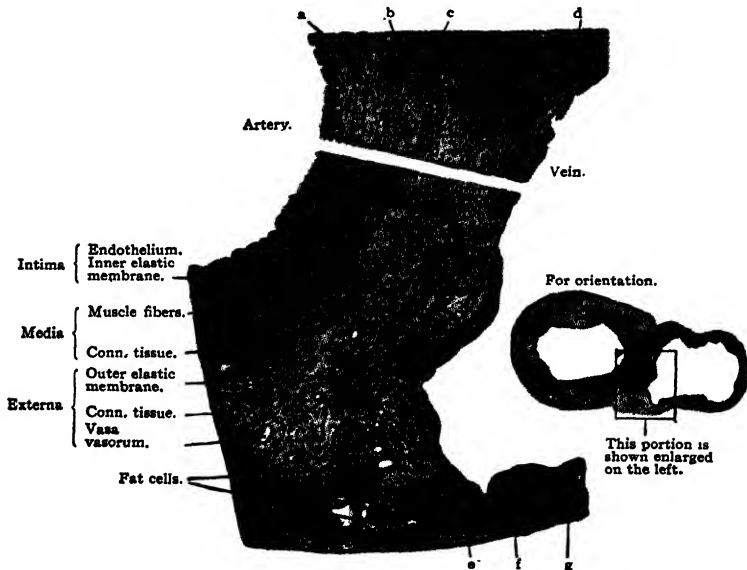


FIG. 196. Histology of the blood vessel. The wall of a blood vessel has an inner layer, the *tunica intima*; a middle layer characterized by connective and muscle tissue, the *tunica media*; and an outer *tunica adventitia* of loose connective tissue. (After Lambert.)

bed may be operative. Both in heat conservation and heat dissipation the adaptive mechanism of the vast capillary bed in the integument plays a leading role.

The Vein. Veins resemble arteries, except for their thinner walls (Fig. 196). The *tunica intima* is a thin endothelium supported by a longitudinally directed meshwork of elastic fibers. The *media*, muscular and fibrous, is relatively thin in comparison with the *media* of the arteries. Circularly arranged smooth muscle fibers largely constitute its substance. Outside this is the *adventitia* of collagenous and elastic fibers with some smooth muscle bundles.

The heart is similar in origin to the blood vessels (Fig. 197). It is distinguished from them by the great development of the cardiac muscular walls, corresponding to the tunica media, and by its contractile functions.

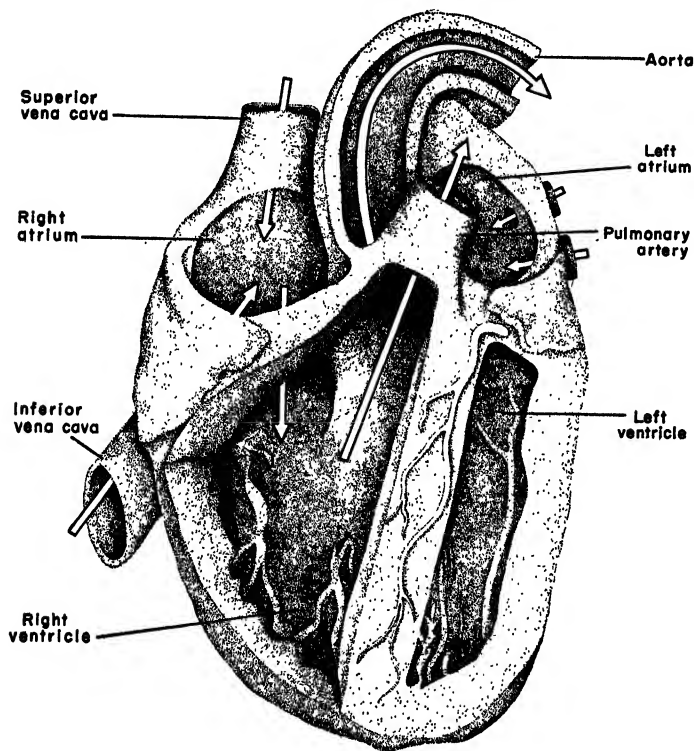


FIG. 197. Interior of heart. Arrows trace the blood flow through the heart. The right atrium receives venous blood via the caval vessels. The blood then passes to the right ventricle and into the lungs by the pulmonary artery. It is returned to the left atrium, whence it passes to the left ventricle and into the artery for distribution to the head and body.

It is generally assumed that the three tunicae of the blood vessels—the intima, media, and adventitia—are homologous to the (1) endocardium, (2) myocardium, and (3) pericardium of the heart, respectively. One theory holds that the entire vascular wall is homologous with endocardium and that myo- and epicardium represent new additions.

The endocardium is the internal heart lining. Its endothelial layer

is continuous with that of the blood vessels. Elastic and collagenous fibers constitute the bulk of the endocardium external to the endothelium. Near its external limits the endocardium is largely a loose connective-tissue network which ties it to the interstitial myocardial tissue. Blood vessels and innervation, including the conduction system of the heart, lie in this portion of the endocardium.

The myocardium is predominantly cardiac muscle held together by interstitial connective tissue. The arrangement of the muscle fibers in an anastomosing network results in simultaneous contraction of the heart as a whole upon stimulation.

The epicardium, or visceral layer of the pericardium, represents the inner wall of the serous membrane of the pericardial sac. It has an outer facing of endothelial serum-secreting cells.

Essentially heart, arteries, capillaries, and veins are a continuous tubular system as noted. The ramifying tubes, lined with endothelium throughout, vary in thickness according to function. Their chief support derives from connective tissue and, exclusive of the heart, from smooth muscle fibers, the latter also serving in adaptively changing the area of the lumen and capacity of the system. The heart represents a specialized part of the tube adapted as a pumping organ with its own peculiar type of musculature. The capillaries, by their small size and thin walls, are permeable membranes, permitting exchange of oxygen, carbon dioxide, food, excretory wastes, and salts.

CIRCULATORY SYSTEM IN THE CHORDATE CLASSES

Amphioxus. The pattern for chordate circulation is laid down in *Amphioxus*, although at a superficial glance this may not be apparent since a heart comparable with that of the vertebrates is absent (Fig. 198).

The homologue of a *sinus venosus* as it has evolved in elasmobranch fishes lies at the caudal level of the gills in *Amphioxus*. This marks the confluence of the *subintestinal vein* and the *ventral aorta*, the latter passing craniad, ventral to the endostyle groove. The ventral aorta has small bulbar enlargements, the *bulbilli*, which agree in number with the branchial arches. *Afferent vessels* extend into the gills from the bulbilli.

Dorsal to the gills the *efferent branchial vessels* unite in paired *radices aortae*, which fuse into a common dorsal aorta beyond the gills. Anteriorly, *carotid arteries* pass from the dorsal aorta to the head. The aorta extends into the tail; branches supply the body wall and the intestine. The returning network unites in part in the *subintestinal vein* and the *postcardinal veins*; the former originates in the caudal vein. The subintestinal vein returns blood to the *liver diverticulum*, where it breaks up

into a capillary network, thus forming a *hepatic portal system*. The *hepatic vein* then returns the blood to the sinus venosus. The blood from the head and anterior part of the body wall is collected in the *anterior cardinal veins*; that from the posterior body walls into the *post-cardinals*. The cardinal veins open into the sinus venosus by the *common ductus cuvieri* on either side, along with a pair of *peribranchial veins*.

Cyclostomes. Cyclostomes have a variable number of gill slits, 6 pairs in *Myxine*, 7 in *Petromyzontia*, 6 to 14 in *Bdellostoma*. Associated with each gill pair is a pair of aortic arches. These unite dorsal to the gills in a series of aortic roots that in turn form the dorsal aorta. The heart is three-chambered, consisting of sinus venosus, atrium, and ventricle. In some respects the relations of the cardinals to the heart more nearly resemble the condition in the mammals than that in the fishes, since the left common cardinal vein disappears in the adult, while right and left anterior cardinals form a precaval vessel. The caudal vein, as in the bony fishes, unites directly with the postcardinals, thus eliminating a renal portal system, *i.e.*, the passage of blood from tail to kidney and thence to the heart.

The definitive vascular system includes a heart (sinus venosus, atrium, ventricle, and conus and bulbus arteriosus), ventral aorta, afferent and efferent branchial vessels, dorsal aorta and its branches, as well as returning veins. Beyond the aortic branches, a capillary network eventually carries the blood to the veins. The venous system has both superficial and deep anterior cardinal and posterior cardinal veins and subintestinal and supraintestinal veins, all returning the blood ultimately to the sinus venosus. A renal portal system is lacking, but the hepatic portal system, present in cyclostomes, is also retained in the remaining vertebrates.

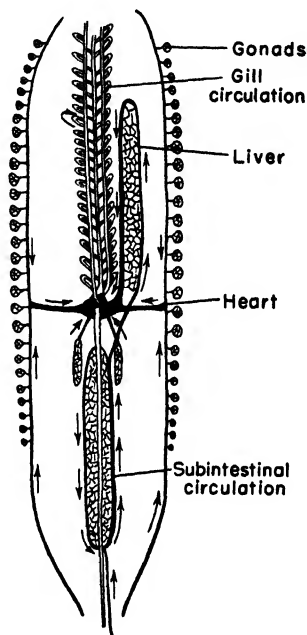


FIG. 198. *Amphioxus* circulation. Blood is distributed from the "heart" to the bulbilli and thence to the gill vessels. From the gills oxygenated blood goes via a dorsal aorta and its branches to the body wall and internal organs, to be returned to the heart by the hepatic portal system.

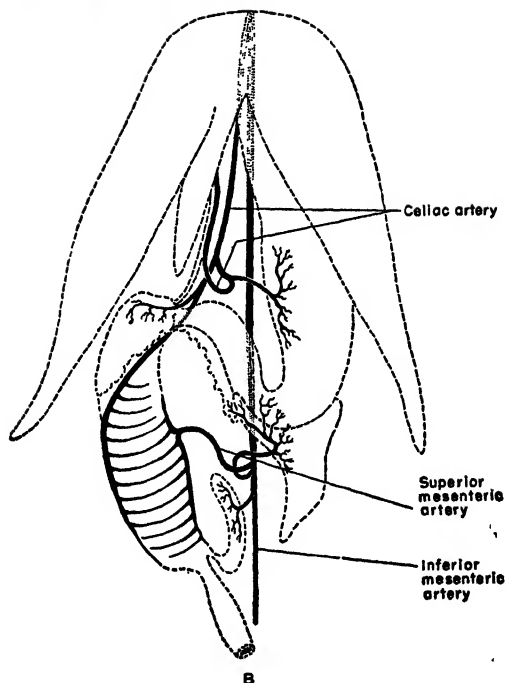
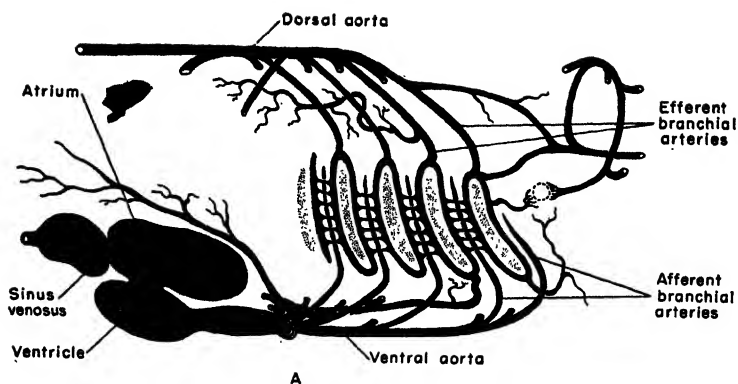


FIG. 199. The elasmobranch arterial circulation. A, blood passes from the ventricle to the ventral aorta and afferent and efferent branchial vessels and thence into dorsal aorta, to be distributed to the head and body; B, the celiac and superior and inferior mesenteric arteries are the great distribution channels for blood to the visceral organs.

The heart lies in a pericardial chamber. The sinus venosus receives the paired cuvierian ducts, the hepatic veins, and the unpaired jugular vein. Blood is passed from the sinus venosus to the single atrium; no valves occur at the sinoatrial junction. From the atrium, blood travels to the single ventricle, which is separated from the atrium by paired atrioventricular valves. From the muscular ventricle a conus and bulbus arteriosus lead to the ventral aorta. Afferent branchial vessels pass to the gills, and efferent branchial arteries re-collect the blood and transmit it to the dorsal aorta, from which it is distributed to the body. Common carotid arteries are directed to the head from the dorsal aorta, and at the posterior margin of the pharyngeal basket they divide into external and internal branches. The external pass ventrally, the internal dorsally to supply the brain and the snout.

A peculiarity of the myxinoid pericardial cavity is the retention of the pronephros within its confines.

Elasmobranchs. The elasmobranch circulatory system, particularly that of the spiny dogfish, is perhaps better known or is at least partially known by more persons than is that of any other cold-blooded vertebrate unless it be that of the frog (Fig. 199A,B).

The heart has a thin-walled *sinus venosus*, which receives blood from the liver and intestine by the *hepatic sinus*; from the tail, kidneys, and gonads by the *posterior cardinal vessels* and sinuses; from the body wall and the pectoral and pelvic girdles by the *lateral abdominal, iliac, and subclavian veins*; from the head and subpharyngeal region by the *anterior cardinal sinuses* and the *jugular veins*. Anterior and posterior cardinals of each side unite at the transverse septum into the *ductus cuvieri*, also called the common cardinal veins, which opens directly into the sinus venosus. All blood that enters the sinus is impure blood. From the sinus venosus it passes into the single *atrium*, the second chamber of the heart. At the sinoatrial junction a pair of endocardial and myocardial folds, or valves, prevent backflow from atrium to sinus venosus.

The *atrium*, also thin-walled and commonly expanded beyond the confines of the wall of the ventricle, has the appearance of two chambers on superficial examination (Fig. 200). A pair of valves separate atrium and ventricle. These valves appear further developed than the sinoatrial valves in that they have lost their fleshy character and have assumed the fibrous appearance of mammalian heart valves.

The *ventricle* is relatively thick-walled. A longitudinal section through its substance reveals a spongy, crevassed structure with a small cavity, the latter communicating anteriorly with the conus arteriosus and posteriorly with the atrium. The *conus*, the conical expansion of the ventricle at its base, leads into the ventral aorta. The *bulbus arteriosus*, some-

times confused with it, is a thickened muscular development of the ventral aorta as it leaves the heart. It occurs in amphibian and in teleost fishes. The number of valves in the conus is variable in the fishes, and the fusion of some of them results in the spiral valve of the Dipnoi and

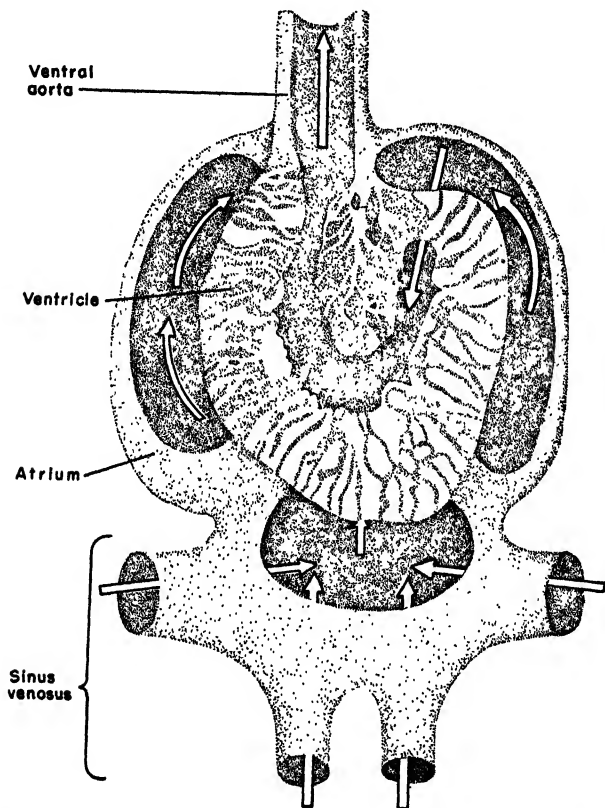


FIG. 200. Elasmobranch heart. The heart consists of a sinus venosus into which all the blood from the body enters. It passes into the single atrium and single ventricle and to the afferent branchial vessels by the ventral aorta.

the amphibians. In the dogfish the conus has three rows of three each of semilunar valves.

The *ventral aorta* penetrates the anterior pericardial wall and extends cephalad deep to the submandibular muscles. Five pairs of afferent branchial vessels extend into the bases of the gills (Fig. 199A). Actually

there are three pairs of main branches; the first and the third divide, while the middle one extends directly to the fourth gill arch. The afferent vessels course along the cartilaginous gill arches and send twigs distally along the gill lamellae.

Efferent collector loops receive the blood after it has traversed the gill lamellae and become oxygenated. These efferent branchial loops unite into four aortic radices, or epibranchial arteries. Each artery arises from the union of a pre- and a posttrematic branch from the anterior and posterior faces, respectively, of the gill pouches. These vessels loop completely around each gill cleft; in addition, cross branches connect post- and pretrematic vessels.

The efferent channels, besides supplying the body with pure blood, also send branches to the head and to the heart muscle itself. Head circulation is effected by external and internal carotids and vertebral, afferent spiracular, and spiracular epibranchial arteries, while the heart muscle is served by coronary arteries.

The *hyoidean epibranchial artery* (common carotid) extends cephalad from the first epibranchial artery at the level of the pretrematic branch of the first functional collector loop. It passes forward and medially along the roof of the mouth and is joined on each side by the small *vertebral artery*, which originates from the first epibranchial artery near the midline, where it joins the aorta. A *stapedial artery* (external carotid) extends laterally from the hyoidean epibranchial, where the latter turns medially. The stapedial artery supplies eye muscles and adjacent structures. Cephalad to this branch, the hyoidean epibranchial is known as the *internal carotid*. It joins its fellow momentarily at the base of the brain, then passes into the skull cartilage to be joined by the efferent spiracular epibranchial artery (ventral carotid). The spiracle no longer functions as a gill, and it receives oxygenated blood via the *afferent spiracular epibranchial artery*, which originates from the pretrematic arm of the first efferent collector loop. From the capillary network of the spiracle, the blood is carried into the *efferent spiracular epibranchial artery*, which continues to the head, where it joins the internal carotid. The blood supply to the head is thus furnished by extensions of the first efferent collector loop and by the vertebral, the hyoidean epibranchial, and the afferent spiracular epibranchial arteries and their divisions.

Still another artery, the true *external carotid* (mandibular), is concerned with arterial circulation to the lower jaw. It originates from the ventral end of the first efferent loop to pass forward along the lower jaw. A pair of *coronary arteries* from the ventral loop of the second efferent

branchial artery extend along the conus arteriosus over the ventricle and the pericardial cavity. They are part of the hypobranchial system, originating in highly variable arteries developed from the ventral ends of the middle collector loops. Their extension into the pericardial cavity forms the coronary system, while the hypobranchial vessels proper supply the muscles of the adjacent region, as well as the esophagus.

The *dorsal aorta* represents the union of the four pairs of epibranchial arteries along the dorsal midline of the pharynx. The paired *subclavian artery*, the first branch to leave the aorta, arises commonly between the roots of the third and fourth pair of epibranchial arteries. The subclavian, after supplying branches to the body wall, terminates in brachial artery to the pectoral fin. One of the body-wall branches, the *ventrolateral artery*, anastomoses with the *epigastric artery*, which ascends in the abdominal musculature. The further distribution of the aorta to the body wall is by somatic or splanchnic branches.

The main branches of the aorta in the abdominal cavity are the celiac, which by gastric, hepatic, pancreaticomesenteric, duodenal, and anterior intestinal branches supplies most of the stomach, liver, and parts of the intestine; the gastrosplenic to the spleen and stomach; the anterior mesenteric to the spiral valve of the intestine; and the posterior mesenteric to the rectal gland. Somatic branches from the aorta include the segmental arteries to the body wall and the paired iliac arteries to the pelvic fins. Visceral arteries are genital, renal, and hemorrhoidal branches, the latter representing small twigs from the iliac arteries. The aorta continues into the tail as the caudal artery.

The pattern of this distribution, although variable in detail, is remarkably constant in its larger outlines. Thus, celiac, anterior and posterior mesenteric, genital and renal, hemorrhoidal, iliac, and caudal arteries are quite predictable in their distribution.

The blood is returned from this peripheral distribution by a system of capillaries and veins (Fig. 201A, B). Beginning in the tail, the *caudal vein* forks at the posterior end of the kidneys and breaks up into veins and sinuses which traverse the kidneys. Blood from the kidneys is collected in the paired *posterior cardinal sinuses*, which, after receiving genital tributaries, enter the *common cardinal veins* (ducts of Cuvier). This complex of renal veins and sinuses together with the postcardinal constitutes the *renal portal system*. This renal portal channel accounts for only part of the returning blood. The blood from the intestines is collected in the large *portal vein* and flows into the *hepatic sinuses* of the liver, to be re-collected and passed directly into the *sinus venosus* via the *hepatic veins*. This aggregate of veins is the *hepatic portal system*. Be-

sides the return from the visceral organs, *lateral abdominal veins* in the abdominal wall return blood to the common cardinal sinuses, receiving small subelavian veins at their junction with the ducts of Cuvier.

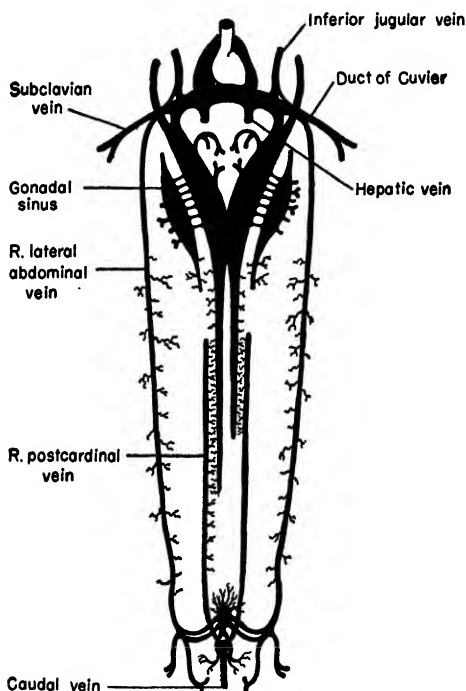


FIG. 201A. The elasmobranch venous circulation. A, the systemic venous channels are paired posterior and anterior cardinals and paired lateral abdominal subclavian veins, with smaller tributaries from the tail, pelvic appendages, and lower jaw region. Caudal, renal, and postcardinal veins form the renal portal system.

Blood from the anterior part of the body returns to the heart by two main routes, the *anterior cardinal trunks*, which originate in the orbital sinuses, and open into the cuvierian ducts at the level of the transverse septum, and the *inferior jugular veins*, which originate in a small jugular sinus lying subcutaneously between the lower jaws.

The primitive pattern, described in some detail here, is recapitulated, with some modifications, in the embryology of the remaining classes, as will be shown. While the stages may be very brief and some steps

omitted, they are nevertheless recognizable. The heart of reptile, bird, and mammal, for example, briefly recapitulates the history of the sinus venosus, the single atrium, and the ventricle. The aortic, pulmonary

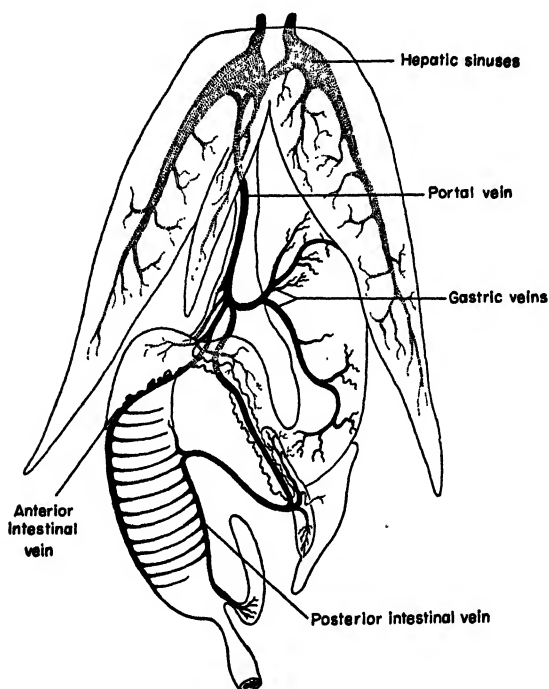


FIG. 201B. The hepatic portal system collects blood from the intestinal tract and returns it to the liver by the portal vein. From the hepatic sinuses it enters the sinus venosus by hepatic veins.

arches, and the carotid circulation, too, may be traced to the type of organization observed in the elasmobranchs.

Teleosts and Dipnoi. The teleost circulation resembles that of the elasmobranchs more closely than it does the dipnoan, although when teleost and elasmobranch are compared, many changes become apparent. Thus, the bulbus arteriosus in teleosts has replaced the conus of the elasmobranchs; a single row of valves at this site is in contrast with the three pairs in the dogfish; a connection is established between the portal and caudal vein, deflecting a part of the blood directly from the tail to

the hepatic portal system; lateral abdominal veins have disappeared; the iliac veins return their blood to the kidneys and thence to the post-cardinals, in contrast to the condition in the elasmobranchs, where they enter the lateral abdominal veins. The aortic arches show fewer changes, although variability in the hyoid region in connection with modifications in gills and in respiratory functions has produced consequent changes in the circulation.

The Dipnoi, as partial lung breathers, undergo profound changes in the circulatory system, in comparison with elasmobranchs and teleosts. This departure from gill breathing has entailed the appearance of a pulmonary artery and a pulmonary vein, the former a branch of the sixth aortic arch, the latter a new development connecting the lung with the left atrium.

The separation of "pure" and "impure" blood in the heart begins in the Dipnoi. This is brought about by the development of a dorsal fold in the atrial and ventricular walls; consequently, when these chambers contract, they become effectively separated into right and left halves. The sinus venosus opens to the right, the pulmonary vein to the left of this fold. Partial fusion of the valves in the conus has created a spiral valve, more or less continuous with the atrioventricular fold. The result is that the blood traversing the ventricle, and partially separated into pure and impure by virtue of having entered either by pulmonary vein or by sinus venosus, remains separated; the pure tends to pass into the carotid and aortic circulation, while the impure is sent into the pulmonary trunk and thence into the lungs.

Other changes in the circulation in comparison with that of the dogfish involve retention of right and left cuvierian ducts but loss of the right anterior cardinal, and the appearance of a postcaval vein which returns blood from the posterior end of the body and enters the sinus venosus between the hepatic sinuses.

Left cardinal and postcaval veins originate in the caudal vein. The latter bifurcates at the posterior margin of the kidney, one arm extending anteriorly as the postcava, the other uniting with the left postcardinal. The abdominal vein originates from the pelvic branches of the iliac veins, while the latter enter the kidneys as renal portal veins. The blood is returned to the heart from the kidney by efferent renal veins, the right by way of the postcava, the left by the postcardinal.

Amphibia. Although the evidence does not indicate a derivation of the Amphibia from a dipnoan stock, the changes in the heart circulation correlated with lung breathing generally parallels the changes observed in the lungfishes (Figs. 202A,B; 203A).

In the heart an interatrial wall divides the atrium into right and left chambers. This wall is generally perforated in Amphibia. The sinus venosus, partly incorporated with the right atrium, now opens into that chamber. It will be recalled that the sinus venosus receives all the un-

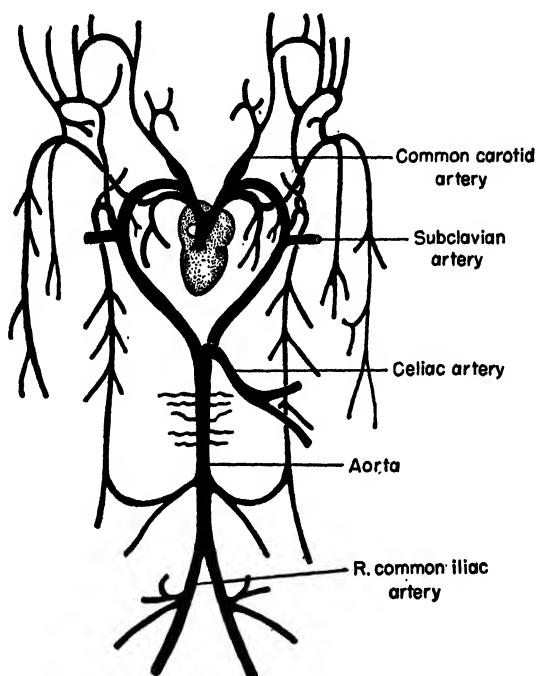


FIG. 202A. Amphibian circulation. A, right and left aortic arches are retained in the Amphibia. The chief arterial channels have their homologues in the fish circulatory system.

oxygenated blood in the elasmobranchs. That same condition prevails in the Amphibia; however, with the division of the atrium, its left half receives oxygenated blood from the lungs by the pulmonary vein. This change in the heart is correlated with the appearance of lungs and takes place during metamorphosis; before that transformation, Amphibia live as gilled forms. Atrioventricular valves effectively separate the divided atrial chamber from the single ventricle. From the ventricle the conus arteriosus extends cephalad. The latter is provided with semilunar valves as well as with a spiral fold; the fold is a fusion of the medial

vertical row of conus valves and plays a significant part in directing the blood as it leaves the heart.

From the bulbus arteriosus, as the muscular extension of the truncus

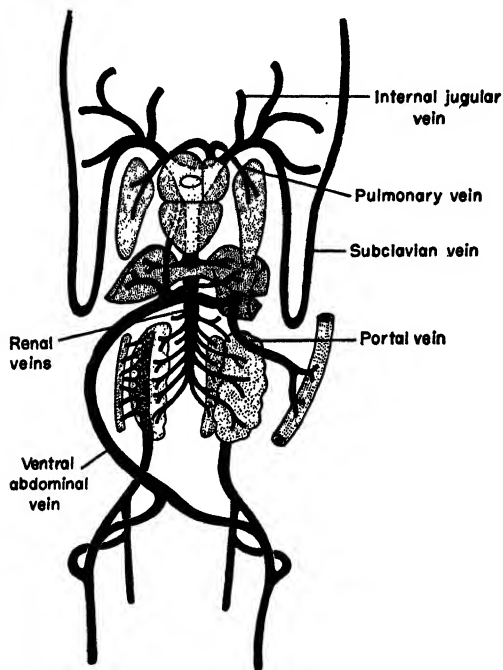


FIG. 202B. The venous circulation has lost the cardinal vessels so prominent in the elasmobranchs.

arteriosus is called, two lateral trunks, which are further divided internally into dorsal and ventral portions, emerge. The dorsal parts are the channels of the pulmonary arteries and correspond to the sixth pair of aortic arches; the ventral portions mark the origin of the carotid arteries to the head and the paired fourth aortic arches to the body. Blood from pulmonary vein and from the sinus venosus, after it enters the divided atrium, may become partially mixed in the ventricle and in the conus. The end result, however, of the presence of interatrial septum and spiral fold in the truncus is to direct the more highly oxygenated blood to the carotid and aortic circuits, while the reduced blood is directed to the pulmonary circuit.

Changes in the venous system, by which blood is returned to the heart, are comparable with those in the venous system of the Dipnoi. A post-cava, originating from the postcardinals, opens directly into the sinus venosus; a single ventral abdominal vein representing the fusion of the two lateral abdominals of the elasmobranchs joins the pelvic veins poste-

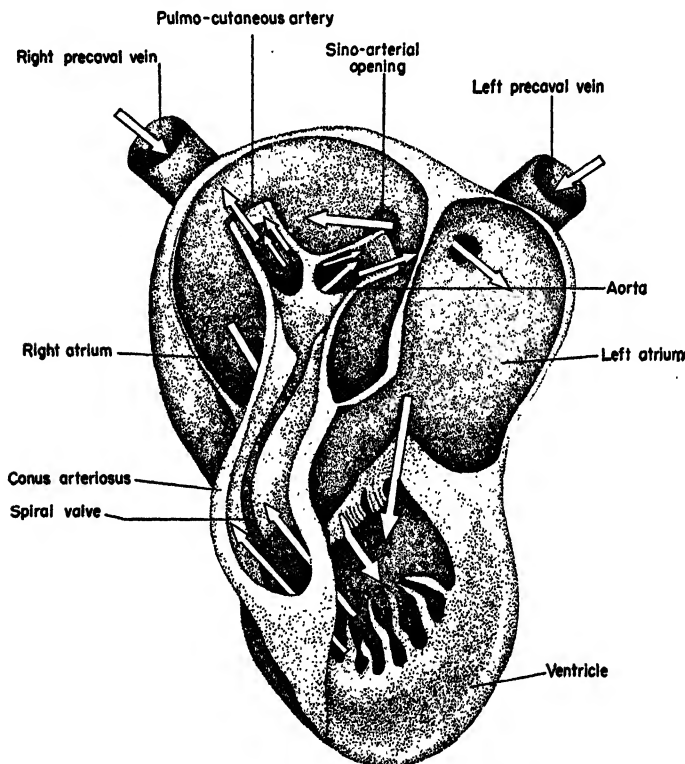


FIG. 203A. Amphibian heart. An interatrial septum has appeared in the amphibian heart; however, blood from the two atria flows into a single ventricle.

riorly and empties into the hepatic vein anteriorly. Hepatic veins transmit the blood from the liver into the postcava. The cutaneous circulation is quite elaborate in many Amphibia. The cutaneous artery, a branch of the pulmonary artery, sends impure blood to the integument for aeration, and vertebral and subclavian branches pass to the mucous membrane of the mouth and pharynx for the same purpose, while paired cutaneous veins return pure blood to the subclavian veins.

Reptiles. In reptiles, changes, particularly in the heart, first indicated in Dipnoi and Amphibia, are carried further (Fig. 203B). The conus arteriosus has disappeared, and fourth and sixth arches are completely divided. The connection between the fourth and sixth arches, the duc-

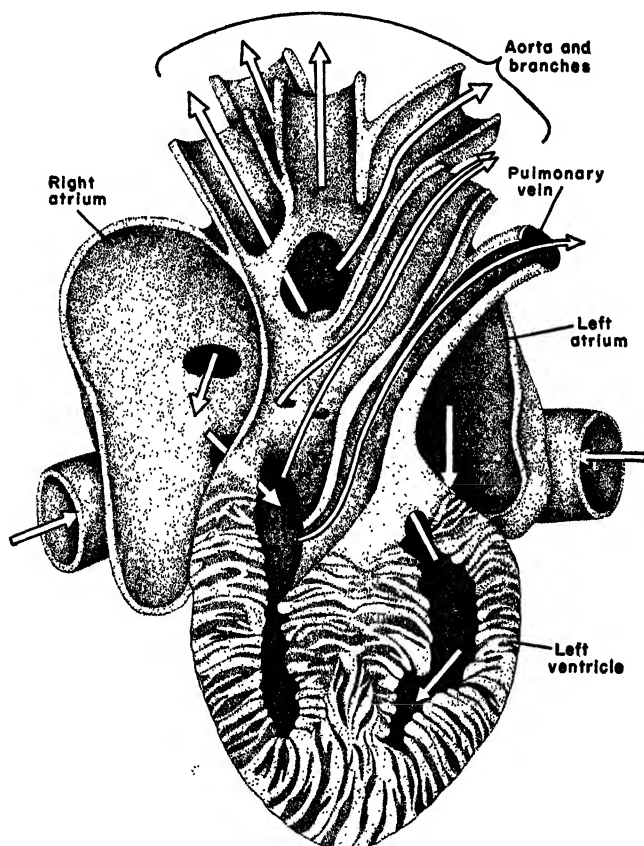


FIG. 203B. Reptilian heart. The heart is incompletely separated into four chambers. The blood after oxygenation returns to the left atrium and is distributed via the aorta, which takes origin in the left ventricle

tus Botalli, persists in the turtles and is of functional significance in re-routing the blood in diving. In lizards it disappears entirely, while in snakes it commonly is converted to the ligamentum Botalli (arteriosum). The interatrial septum is complete, and an interventricular septum has

appeared, which partially separates the ventricle into right and left chambers in the reptilian orders with the exception of the Crocodilia. In this order, the septum is complete, save for an opening just above it, the foramen Panizzae, which permits communication between pulmonary and aortic trunks. The sinus venosus has become more completely incorporated in the right atrium than it was in the Amphibia.

In spite of these advances, and advances they may be called, since they produce a more effective separation between oxygenated and non-oxygenated blood, some mixing of blood is still possible in the heart. In the Chelonia, for example, right and left fourth aortic arches open from the base of the ventricle. The right fourth arch lies farthest to the left in the ventricle and consequently receives the purest blood, which it transmits to the carotid circulation. It continues around the heart and joins the left below this level. The left fourth arch originates to the right of the preceding and consequently lies more in line with the stream of venous blood as it leaves the ventricle. This left arch joins the dorsal aorta caudad to the heart as indicated, but before this junction it gives off the celiac artery, which in consequence receives mixed blood. The sixth, or pulmonary, arch stems far to the right on the ventricle and carries the least pure blood, since it is directly in line with the right atrium, into which opens the sinus venosus. Since this blood is destined for the lungs, the arrangement of this particular channel is in keeping with greater circulatory efficiency.

The common carotid arteries originate from the right aortic arch in reptiles. As indicated, the right aortic trunk arises from the left side of the ventricular base; hence it receives the oxygenated blood.

The venous circulation of amniotes is more complicated than that of the anamniotes, a condition determined by the presence of the allantois. The allantois is a respiratory outgrowth from the cloacal wall. Presumably the amnion and chorion, since they cover and separate the embryo from rapid contact with the air, make a secondary respiratory organ like the allantois necessary. The yolk-sac circulation alone appears inadequate, and a system of omphalomesenteric veins and arteries becomes associated with the allantois, which in mammals forms the basis for the placental circulation. The abdominal vein, derived from the umbilical vein, may be paired and returns blood to the portal vein. A large postcava returns blood from the caudal veins and the kidneys. The hepatic vein also opens into this caval vessel. Both common cardinal (cuerian ducts) veins are retained and open into the sinus venosus.

Birds. The bird heart differs from the reptilian in its relatively greater size and the more complete incorporation of the sinus venosus with the

right atrium, although the sinus is never entirely absorbed (Figs. 204, 205). Internally it remains separated from the atrium by the relatively large *valvulae venosae*. Internally, other significant features of the

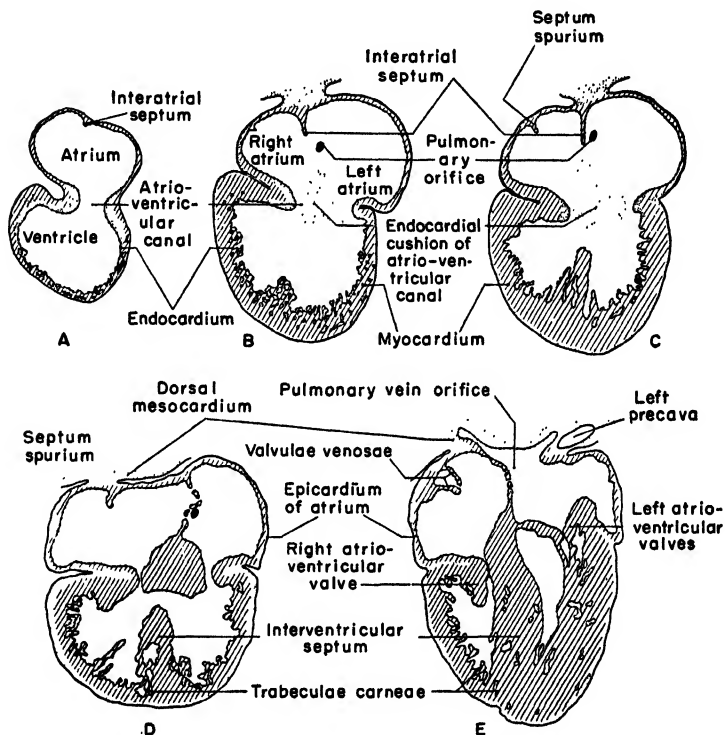
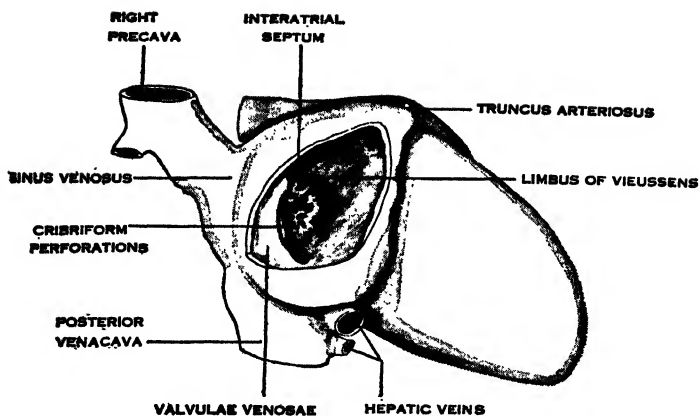
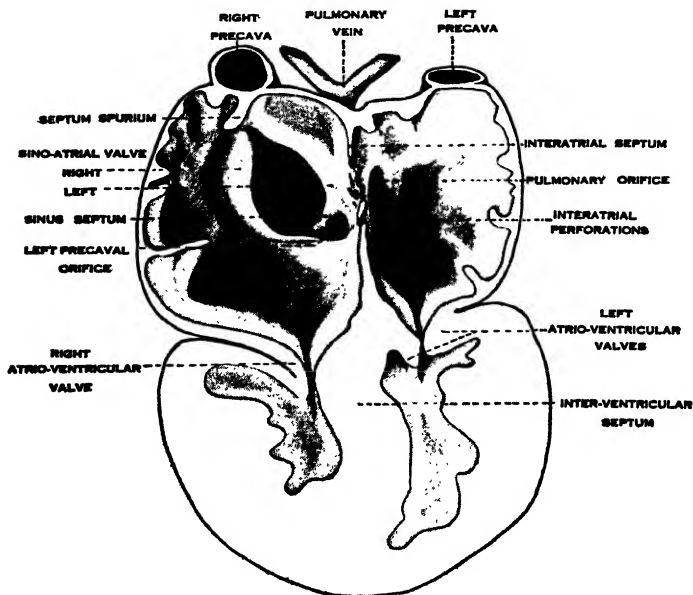


FIG. 204. Stages in the development of the bird heart. Semischematic fronta sections of the chick heart at five different ages, to show the development of the interatrial septum and the endocardial cushions (15). A, at 65 hours with the interatrial septum barely indicated; B, at 96 hours, showing descent of the septum and presence of the endocardial cushion; C, at $4\frac{3}{4}$ days; the septum has almost fused with the endocardial mass; D, at 5 days; the septum and endocardial cushion tissue have fused, and secondary perforations have appeared in the septum; E, at 7 days; both the interatrial septum and the interventricular have fused with the endocardial mass.

bird heart are the great pulmonary fold, or valve, partially incorporated with the interatrial septum; the single atrioventricular valve between right atrium and right ventricle; and the system of muscular arches in



A



B

Fig. 205A and B. Stages in the development of the bird heart. A, right lateral view of a wax plate reconstruction of a 7-day chick heart, with a part of the right atrial wall removed to expose the cribriform perforations in the interatrial septum, the valvulae venosae, and the prominent limbus of Vieussens (30). B, frontal section through an 11-day chick heart, based on wax plate reconstruction (17, 3). Note especially the prominent valvulae venosae, the sinus septum, and the relation of the left preceaval and pulmonary orifices to the perforated interatrial septum.

the atrial walls, which may have a functional significance during atrial systole.

Aortic and pulmonary trunks are separated early in development, and

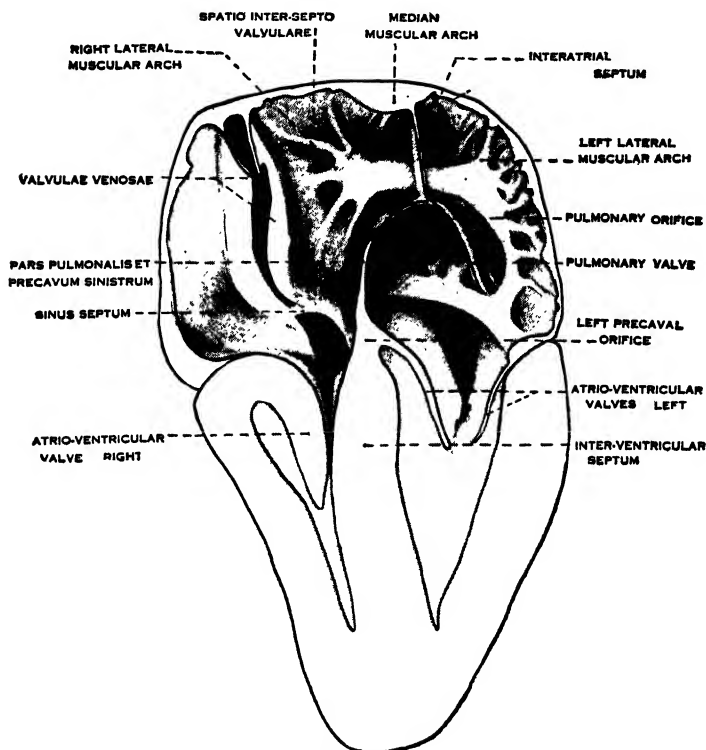


FIG. 205C.

FIG. 205C. Stages in the development of the bird heart. Frontal section through an adult fowl heart to show the relation of the primary part of the interatrial septum to the pars cavopulmonalis and the small size of the primary part of the interatrial septum as compared with the secondary portion (2.3). Note the retention of the valvulae venosae and the sinus septum in the adult. The figure also shows the difference in size of the two atria, the atrial muscular arches, and the right atrio-ventricular valve.

normally the right aortic arch persists, while the left disappears, the converse of the mammalian condition (Fig. 206B). Glenny has recently found that both right and left fourth arches are retained much more commonly in birds than has been generally assumed.

The venous system in its outlines follows the reptilian pattern. The hepatic portal system is retained in its entirety, while the renal portal system is partially functional with an optional route offered the blood returning from the caudal and the hind-limb regions (Fig. 206A). The hepatic portal system is formed by superior, inferior, mesenteric, and gastric veins. These unite in a common hepatic portal vein and collect blood from the various parts of the intestine and stomach. After passing through the liver, this blood is re-collected in hepatic veins which enter

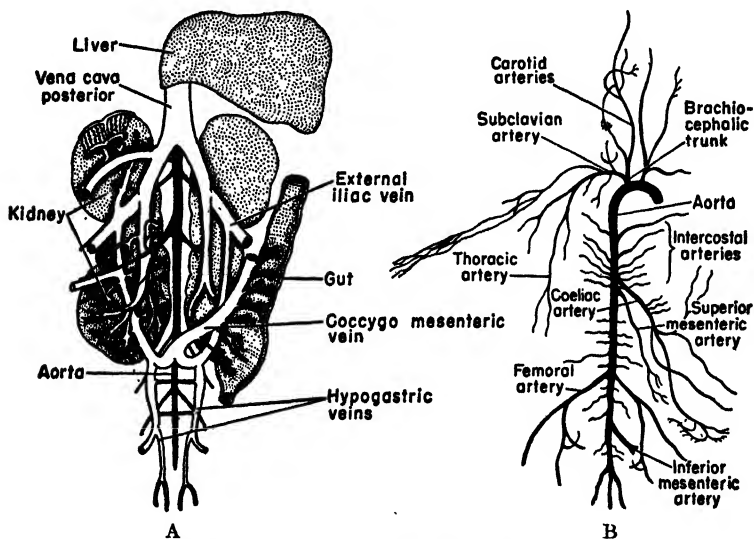


FIG. 206. Bird circulation. A, arteriovenous circulation to the kidney and liver in the bird; B, the aorta of the bird arches to the right in its descent to the abdomen. (Redrawn from Stressemann.)

the postcava. The latter vein enters the right atrium. The postcava begins at the junction of the iliac and femoral veins. Caudad to this the iliacs, known as the renal portal veins, overlie the kidneys and through small branches permit the entry of blood into the excretory organs. Right and left renal portal veins anastomose caudad to the kidney and receive both caudal and hypogastric branches. Blood may pass from the renal portal veins into the kidneys, as indicated, or continue in the iliacs to their junction with the postcava. If it passes into the kidneys, it is returned into the renal veins, which are small tributaries to the postcava.

heart wall, as already described, consists of an endocardium, a thin epithelial lining tissue; a myocardium, which is the cardiac muscular layer and constitutes by far the greater bulk of the heart; and the epicardium, or outer serous layer, which is another epithelial layer.

The mammalian heart is supplied by right and left *coronary arteries*, the first branches of the aorta, emerging directly above the aortic valves from slight aortic dilatations, the *aortic sinuses*. The coronary vessels are variously distributed as circumflex, marginal, and descending branches. The venous return of cardiac blood, by way of the coronary sinus, opens into the medial wall of the right atrium below the level of the interatrial septum.

At the site of the *foramen ovale*, the fetal interatrial foramen, is the *fossa ovalis*. This is an oval depression at whose upper margin a communication with the left atrium sometimes persists in the adult mammalian heart.

In lower vertebrate animals the heartbeat is initiated in the sinus venosus, and since there is muscular continuity throughout the chambers, the contraction impulse passes to atrium, from atrium to ventricle, and, if a conus is present, to the conus. In each chamber the beat is a separate occurrence. At the mammalian level this ancient sequence is not obliterated, although the two atria beat as one, just as do the two ventricles. The junction of the right atrium with the superior vena cava marks the remnant of sinus venosus tissue, the *sinoatrial node* (Keith-Flack node), where the beat is initiated. This node joins with a band of modified muscle tissue, the *atrioventricular bundle* (bundle of His). The bundle arises near the opening of the coronary sinus and passes upward and forward from a nodal enlargement along the interventricular septum after branching into two trunks, one extending along the interventricular walls of the right, the other along the same wall along the left ventricle. These modified muscle fibers terminate in special *Purkinje fibers* at the bases of the papillary muscles.

The atrioventricular bundle is more easily identified in sheep and certain other ungulates than in carnivores and primates. The bundle, surrounded by a connective-tissue sheath, also carries sympathetic and parasympathetic nerve fibers from the atrium to the ventricles. The Purkinje fibers are peculiar muscular fibers, extending into the moderator band and the atrioventricular bundle and along the atrial and ventricular walls. Each cell of the bundle contains one or several nuclei and a granular cytoplasm with clear fibrous extensions and somewhat larger than ordinary cardiac muscle cells.

Aortic Arches. With the complete division of the heart into left arterial and right venous sides, the pulmonary artery and aorta, too, become completely separated in the adult (Fig. 208A, B). The latter two trunks, as noted, represent the *sixth* (pulmonary) and the *fourth* (aorta) aortic arches. The *fifth* arch is functional in embryonic life as a short channel by which blood by-passes the lungs. Since lung breathing

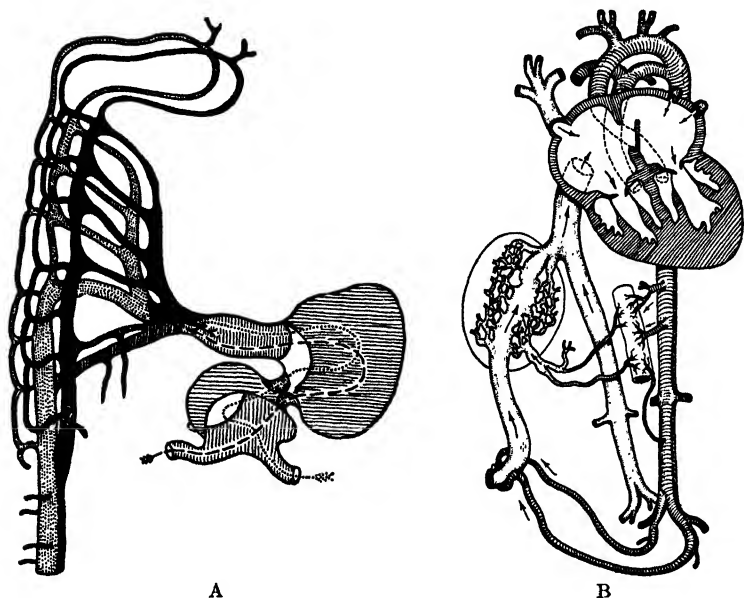


FIG. 208. Development of human circulation. Fetal circulation. A, aortic arches are formed in embryonic development. Arches 1 and 3 supply the carotid circulation; arch 4 is the aortic arch; arch 6 becomes the pulmonary artery. B, interatrial foramen persists until birth. The umbilical veins transport blood from the placenta to the heart; aortic branches, including umbilical arteries, carry blood to the body and to the placenta. (Redrawn from Patten.)

does not begin until after hatching or after birth, the volume of blood passing to the lungs during the developmental period is small. Known as the *ductus Botalli* during this patent period, the fifth arch is converted, as mentioned earlier, to the ligamentum Botalli (arteriosum), when its lumen becomes closed. This ligament supports and unites the bases of aorta and pulmonary arches in adult life.

The *pulmonary artery* bifurcates dorsad to the aortic arch, to supply the right and the left lungs with venous blood for oxygenation. The

right branch is usually slightly longer than the left because of the position of the heart to the left of the midline. By repeated division, the vessels are reduced to the capillary stage to be associated with the air pouches, or alveoli, of the lungs. The nutritional blood supply to the lungs (not to be confused with the blood to be aerated) is furnished by bronchial arteries which branch directly from the thoracic aorta or from the intercostal arteries.

The *aorta* (fourth aortic arch) is the great trunk line from which is distributed the oxygenated blood to the entire body. Beginning at the left ventricle, it extends unbrokenly into the pelvis, where it divides into two terminal branches, the right and left common iliac arteries. For descriptive purposes it is conveniently divided into ascending, descending, thoracic, abdominal, and caudal segments.

The first branches of the aorta are invariably the *coronary arteries*, whose openings immediately above the semilunar aortic valves have been noted. In some animals a single coronary vessel leaves the aortic trunk; more frequently right and left branches emerge directly from the aorta.

Since the aortic arch bends to the left, an asymmetry of the branches anterior to the heart results. Various types of arterial distribution have evolved in the vertebrate series, correlated with this asymmetry. In the generalized type, the right aortic arch, retained as a remnant, comprises the root of the right innominate artery. This divides into the right subclavian, which supplies neck, shoulder, and arm; and the right common carotid, to the neck, face, and brain. Great variations in the origin of carotids and subclavian arteries exist. The bats show the nearest approach to symmetry in the innominate distribution. Here a right and a left innominate trunk each subdivides into a subclavian and a common carotid artery. Another variant appears in certain carnivores and rodents in which a right innominate gives off both carotids and right subclavian, while the left subclavian emerges independently from the trunk. A third type common to many primates, man and rodents, consists of a right brachycephalic (innominate), which includes right subclavian and right carotid, while left carotid and left subclavian emerge separately. Elephants and beavers have a common carotid trunk between independent right and left subclavians.

In ungulates a single brachycephalic trunk gives off right and left subclavians and also a common carotid trunk, which divides subsequently into right and left halves.

A general description of the arterial system cannot hope to touch on all the individual changes in the great chordate classes. The distribution of arterial blood in the mammals follows quite closely the following outline.

Carotid Arteries. The *common carotids* springing from the arch of the aorta usually divide high in the neck into external and internal carotid arteries. The external send out thyroid, lingual, ascending pharyngeal, superficial temporal, external, and internal maxillary, occipital, and posterior auricular branches. Among these the internal maxillary artery has some meningeal distribution. The internal carotids, on the other hand, pass to the floor of the brain case, and their main distribution is cerebral and chorioidal.

The *subclavian arteries*, in mammals, are defined as extending from their origin on the aorta to the outer border of the first rib. They give off vertebral, thyrocervical, and internal mammary, and costocervical branches. Of these the paired vertebrales run a rather unique course: each enters the transverse foramen of one of the lower cervical vertebrae (sixth in man and dog) and passes to the head via the foramen magnum, after traversing the remaining transverse foramina. The confluence of right and left vertebral arteries on the ventral surface of the medulla forms the basilar artery, which anastomoses with the internal carotid artery through anterior and posterior communicating branches, to form the circle of Willis, enclosing infundibulum and optic chiasma and mamillary bodies. The internal mammary branch of the subclavian artery, too, has an interesting course. It passes on each side along the under-surface of the ribs, just lateral to the sternal plate, and descends along the abdominal wall, giving off intercostal branches as it moves downward. It makes a direct and easily identified anastomosis with the inferior epigastric artery, the latter a branch of the external iliac in the lower abdomen. The distribution of thyrocervical and costocervical arteries is implied in their names.

The *axillary artery*, the continuation of the subclavian trunk, begins at the outer border of the first rib and extends to the lower border of the tendon of the *teres major* muscle. Its branches are distributed primarily to the muscles of the shoulder and upper arm and the shoulder-joint capsule. Its chief branches are supreme thoracic, thoracoacromial, lateral thoracic, subscapular, and posterior and anterior humeral circumflex arteries.

The *brachial artery* is the extension of the axillary to the upper arm. Its lower limit is its bifurcation into radial and ulnar arteries at the hollow of the elbow (cubital fossa). From the brachial artery are given off collateral, muscular, and nutrient branches; from the radial and ulnar, carpal, volar, and digital vessels.

The above vessels mark the chief arterial distribution to head, neck, shoulder, arm, and upper chest. The descending aorta has a dual dis-

tribution in the thorax (Fig. 209); part of this, the parietal, is directed to the intercostal, subcostal, and diaphragmatic region. The remainder, designated as visceral, consists of pericardial, bronchial, esophageal, and mediastinal branches. As it passes the diaphragm and continues into the abdomen, the aorta, now the abdominal aorta, has a further visceral

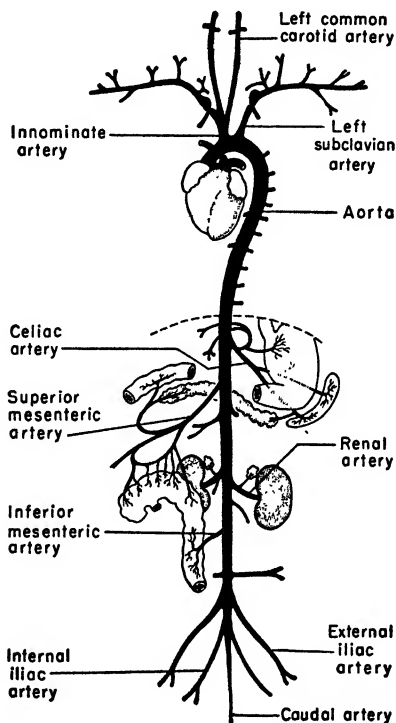


FIG. 209. Mammalian arterial circulation. Arterial channels in the cat. (*Redrawn from Eddy, Oliver, and Turner.*)

distribution to the intestines by celiac and superior and inferior mesenteric arteries and to the adrenals, kidneys, and gonads by adrenal, renal, spermatic, and ovarian vessels. Parietal branches pass to the diaphragm by the inferior phrenic, to the lumbar and sacral muscles by lumbar and sacral branches.

At the sacral level the aorta bifurcates into common iliac trunks, which extend into the lower extremity as external iliacs, after giving off a pair of internal iliac (hypogastric) arteries to the pelvic contents (Fig. 209).

Besides supplying the thigh and lower limb, each external iliac artery sends an inferior epigastric branch upward along the abdominal wall. This branch continues as the superior epigastric and anastomoses with the internal mammary artery as indicated. The femoral artery, a continuation of the external iliac in the thigh, becomes the chief source of blood distribution to the leg through its branches. In its course it passes from the anterior to the posterior surface of the thigh at the level of the popliteal fossa and continues as the popliteal artery. In the fossa it divides and sends an anterior tibial artery to the anterior aspect of the shank and a posterior which divides into a medial posterior tibial and a lateral peroneal artery. The posterior tibial finally bifurcates near the heel into lateral and medial plantar branches which anastomose and send out digital branches to the toes.

The internal iliac artery (hypogastric) is confined largely to the pelvis, where it supplies the viscera and the reproductive organs. It also sends some branches to the perineum, the gluteal muscles, and the adductors of the thigh.

Tabulation of Arteries. Table 11 indicates in condensed form the chief arterial channels in the human body; with minor exceptions, it also applies to the remaining mammals.

Table 11 includes most of the prominent arteries in the typical four-footed mammal. It should be emphasized that each glandular, muscular, and skeletal structure or system has its adequate blood supply. It should be noted further that extensive anastomoses exist between one artery and another. Thus, the carotid circulation, if shut off on one side of the head, is supplied by the other side, as well as by the vertebral, etc., or if the internal mammary artery is ligated high in the thorax, the blood passes upward by the inferior and superior epigastric arteries. Around the joints, various accessory arteries provide auxiliary channels which may be greatly expanded, should the need arise through accidental loss of the main vessels. These anastomoses are of very practical interest to the surgeon, who frequently is compelled to ligate large vessels. Unless the subsidiary channels develop sufficient capacity to supply the affected part, necrosis sets in. Generally, the arterial channels dwindle gradually to capillaries before the blood is collected in veins. In the hands and feet of land animals, direct anastomoses between arteries and veins occur. This apparently is an adaptation for maintenance of warmth in the extremities.

Mammalian Veins. The veins of mammals exhibit no outstanding peculiarities (Fig. 210). They are subdivided into systemic veins which convey reduced blood to the right side of the heart, pulmonary veins which return oxygenated blood to the left atrium, and hepatic portal

TABLE 11. CHIEF ARTERIAL CHANNELS OF MAMMALS

Paired common carotids

External carotids

Neck

Thyroid

Lingual

Ascending pharyngeal

Face

External maxillary

Occipital

Head

Posterior auricular

Internal maxillary

Superficial temporal

Internal carotids

Ophthalmic branches—meningeal

Cerebral

Chorioidal

Paired subclavian arteries

(From origin on aortic arch to outer border of first rib)

Vertebral

Thyrocerivical trunk

Internal mammary

Costocervical axis

Axillary artery

(Outer border first rib to lower border tendon of teres major muscle)

Supreme thoracic

Thoracoacromial

Lateral thoracic

Subscapular

Posterior humeral circumflex

Anterior humeral circumflex

Brachial artery

(Tendon of teres major to elbow, where it divides into radial and ulnar arteries)

Ulnar collateral

Muscular

Nutrient

Anastomosing arteries

Carpal and volar arches

Digital arteries

Descending aortae

Thoracic

Visceral

Pericardial

Bronchial

Esophageal

Mediastinal

Parietal

Intercostal

Subcostal

Superior phrenic

TABLE 11. CHIEF ARTERIAL CHANNELS OF MAMMALS (*Continued*)

Abdominal

Visceral

Celiac

Superior mesenteric

Inferior mesenteric

Middle suprarenals

Renals

Internal spermatics

Ovarian (female)

Parietal

Inferior phrenics

Lumbar

Middle sacral

Terminal

Common iliacs

Internal iliacs (hypogastric)

Iliolumbar

Lateral sacral

Superior gluteal

Inferior gluteal

Obturator

Pudendal

Vesical

Middle rectal

External iliacs

Inferior epigastric

Deep iliac circumflex

Femoral

Superficial epigastric

Superficial iliac circumflex

Superficial external pudendal

Deep external pudendal

Muscular

Profunda femoris

Highest genicular

Popliteal

Anterior tibial

Posterior tibial recurrent

Fibular

Anterior tibial recurrent

Muscular

Anterior medial malleolar

Dorsalis pedis

Arcuate

Deep plantar

Posterior tibial

Peroneal

Nutrient

Muscular

Posterior medial malleolar

Medial and lateral plantar

system. Venous sinuses in the body are peculiar in that with some exceptions they are confined to the inside of the skull and represent canals between the layers of the dura mater. They have the customary endothelial lining of blood vessels.

The peculiar nature of the portal vein or, better, portal system should be mentioned, since it represents a capillary-bed interruption in a vein.

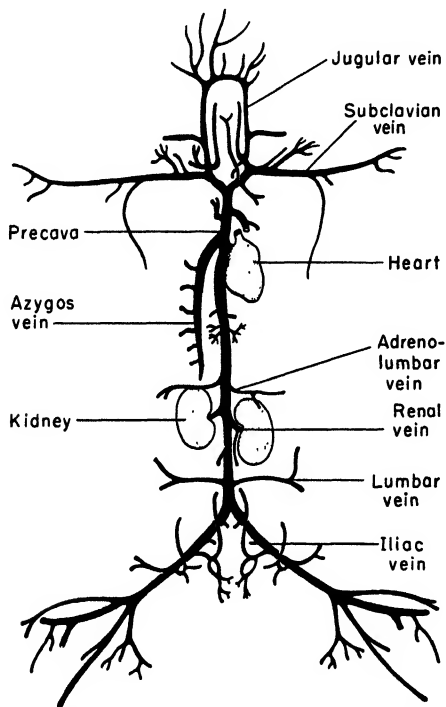


FIG. 210. Mammalian venous circulation. *

In the hepatic portal system, for example, the venous blood from the intestine is collected in the large portal vein, which enters the liver and is broken up into hepatic sinuses and capillaries; the blood is re-collected in the hepatic veins, whence it enters the heart. In other words, the blood passes from capillaries in the intestine to intestinal veins, to the hepatic portal vein, to capillaries in the liver and to the hepatic veins.

Valves are important in preventing the backflow of blood in the venous system. Formed by a folding or reduplication of the intimal layer of

the veins with additional connective-tissue strengthening, they appear in most of the larger venous channels. They are semilunar in shape and usually arranged in pairs, more plentiful in the lower extremities, where the blood has to be lifted against gravity, and generally absent in spinal and cerebral veins, although they do occur in the jugulars.

Both arteries and veins possess their own nutritional, respiratory, and regulatory blood supply, through small *vasa vasorum* which form delicate plexuses about their walls. No part of the body is omitted in the distribution of blood.

The profound influence of the blood is generally known, but only recently Bronk and his coworkers have shown that the proximity of an arteriole or capillary to a given region in the brain determines the rate of the nervous activity of that region. Thus, the nerve cells enjoying a favored position near such a blood source have a higher metabolic rate and a higher performance level than those more distantly situated.

The constancy of the vascular channels in the mammalian series is remarkable when one considers the great range in size and weight, the great differences in behavior expressed in energy release. The largest heart which the author has been able to examine was obtained in the dissection of a 130,642-lb. sperm whale. This heart weighed 842 lb. Except for its size it showed the same comparable parts which a heart of a 14-gm. mouse possesses. Aorta, pulmonary artery and vein, and superior and inferior vena cava showed the same relationships to the heart as they do in the mouse.

DYNAMICS OF THE CIRCULATION

The description of the circulatory system has left untouched its dynamic characteristics. Advances in heart structure and vascularization have been indicated, and since animals are causal, by which we mean that they obey the laws of cause and effect in their organization, we should be able to read many of the characteristics of the animal from heart size and blood volume alone. Conversely, when we observe them in action and see their bodies propelled as fast as 60 miles per hour on land and at higher speeds in the air, we expect heart development, blood volume, and musculature to reflect this ability to utilize and transform energy.

Heart-Body Weight Relations. Table 12, based upon a few dissections, shows the percentage of heart mass to body mass in animals ranging from 345 to 878 gm. in body weight. The highest heart-body weight ratio is observed in the buzzard; the lowest in the fish. The mammals show a fairly constant ratio.

TABLE 12. HEART-BODY WEIGHT RATIOS

Animal	Sex	Body wt., gm.	Heart wt., gm.	Ratio $\frac{\text{Heart wt.}}{\text{Body wt.}} \times 100$
Electric ray (<i>Torpedo torpedo</i>).....	M	345	0.22	0.064
Pike (<i>Esox lucius</i>)	F	374	0.56	0.150
Bullfrog (<i>Rana catesbiana</i>).....	M	519	1.65	0.318
Black snake (<i>Coluber constrictor</i>) .	F	286	0.96	0.333
Buzzard (<i>Cathartes aura septem-</i> <i>trionalis</i>).....	M	495	10.24	2.068
House cat (<i>Felis domesticus</i>)	M	576	3.00	0.521
Coati (<i>Nasua narica panamae</i>)..	M	399	2.00	0.501
Armadillo (<i>Dasypus novemcinctum</i> <i>fenestratus</i>).. . . .	M	471	2.30	0.488
Opossum (<i>Didelphis marsupialis</i> <i>etensis</i>)...	M	666	3.40	0.480
Guinea pig (<i>Cavia cutleri</i>).....	M	456	1.86	0.406
Rabbit (<i>Sylvilagus gabbi mes-</i> <i>serius</i>)	M	439	2.00	0.455
Hyrax (<i>Heterohyrax brucei</i>).....	M	750	3.63	0.485
Richardson's ground squirrel (<i>Ci-</i> <i>tellus paryii paryii</i>).... .	M	878	5.85	0.666

TABLE 13. INCREASE OF HEART SIZE WITH REFERENCE TO BODY WEIGHT

Animal	Sex	Body wt., kg.	Heart wt., gm.	Heart wt. Body wt. $\times 100$
Shark, sand (<i>Carcharias littoralis</i>)..	F	123	115	0.09
Crocodile (<i>Crocodilus americanus</i>)..	M	134	134	0.10
Turtle (<i>Chelonia midas</i>).....	F	114	180	0.16
Man.....	M	79	331	0.42
Swine (<i>Sus scrofax</i>).....	M	60	400	0.66
		113	452	0.40
Seal (<i>Erignathus barbarus</i>).....	F	110	515	0.47
Lion (<i>Felis leo</i>).....	M	118	713	0.62
Porpoise (<i>Phocaena phocaena</i>) . . .	M	114	738	0.65
Hartebeest (<i>Bublis cokei cokei</i>)....	M	134	875	0.65
Guatemala horse, gelding (<i>Equus</i> <i>caballus</i>).....		123	850	0.66
Lion (<i>Felis leo</i>).....	M	126	1,078	0.86
Caribou, barren ground (<i>Rangifer</i> <i>arcticus</i>).....	M	128	1,086	0.85
Ostrich (<i>Struthio camelus massai-</i> <i>cus</i>).....	M	123	1,205	0.98

TABLE 14. CARDIAC COEFFICIENTS

Name	Number	Heart coefficients
Bony and cartilaginous fishes.....	69	0.0542
Bullfrogs.....	6	0.0811
Reptiles.....	77	0.0907
Rodents and insectivores.....	485	0.1328
Primates (exclusive of man).....	223	0.1561
Human males, white.....	7	0.2441
Birds.....	236	0.2605
Human males, Negro.....	4	0.2703
Ungulates.....	1119	0.2951
Carnivores.....	72	0.2952
Cetacea.....	7	0.3722

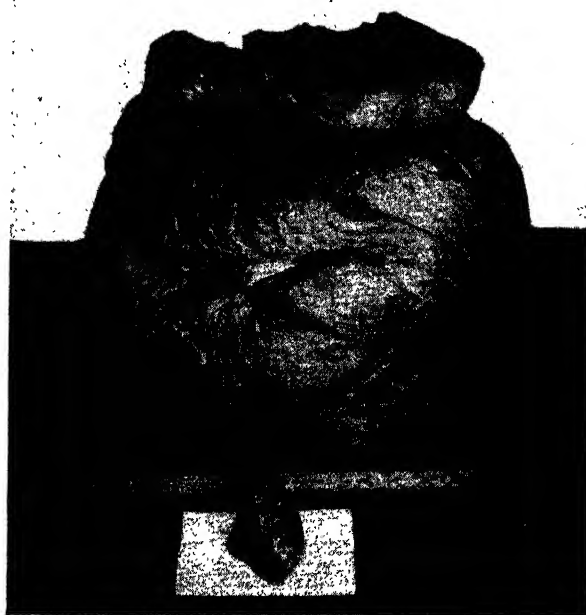


FIG. 211. Photograph of the heart of a humpback whale, *Megaptera nodosa*, and a human heart. The whale heart weighed 472 lb. when removed from the specimen. The animal weighed 82,000 lb. The human heart weighed 0.866 lb.; the person from whom it was removed weighed 142 lb. (One whale heart in the Crile series weighed 842 lb.; the specimen weighed 130.942 lb.) ;

Domestication affects many organs, including the heart. Darwin, Klatt, and others have pointed out that brain size tends to decrease with domestication. The author's own data based on several thousand observations point to similar changes for the heart. Thus, domestic cattle and pigs show heart-body weight ratios of between 0.30 and 0.44, compared with the wild African buffalo, 0.53; impala, 0.73; Barren Ground caribou, 0.85. Table 13 shows the increasing heart ratios in a number of the larger vertebrates, including man.

Another measure of relative heart size may be made in terms of the so-called cardiac "coefficient." This coefficient is the term b in the equa-

TABLE 15. HEART RATES IN VARIOUS ANIMALS

Animal	Body wt., gm.	Heart rate, per minute
Boa constrictor	6,800	15-25
Common fowl	1,980	312
Duck, domestic	2,304	212
Buzzard	658	301
Sparrow	30.5	460
Crow	337	342
Rabbit	2,642	368
Horse	460 kg.	28
Elephant	3,000 kg.	22-28
Dog	10 kg.	140
Man	70 kg.	78
Whale, 30 m. long	265,000 kg.	5.3*
Whale, 25 m. long	152,000 kg.	6.4*
Sperm whale, 22 m. long	58,500 kg.	15-18

* Estimated.

tion $Y = bX^*$. The coefficient is an index of the degree of heart development, taking into account the great differences in body mass. Table 14 shows such cardiac coefficients.

The data in Table 14 simply imply that the ungulates, carnivores, and Cetacea, for example, are on a much higher level of heart development than are the fish or the amphibians (Fig. 211). The birds do not fare so well. The group included over 100 common fowls, and domestication apparently has been a factor in reducing their relative heart weights. Wild bird species show a coefficient of approximately 0.3000. If the heart coefficients have meaning, they indicate that correlated with the increase of the coefficients is a greater amount of activity and a larger expenditure of energy.

The rate of heartbeat also varies greatly in animals. As a rule the rate decreases with increasing size. In Table 15 are a few records taken directly from animals or from the literature.

The data in Table 15 presumably represent resting pulses. With increasing bodily activity, this rate is greatly augmented. In the case of the sperm whale listed, the rate was approximated by watching the spurts of blood issuing from a wound in its side as it was towing a 60-ton boat, obviously not a resting pulse rate. The data on the remaining whales are taken from the literature. Just how the resting rates were determined in some instances is not stated.

BLOOD

The function of the vascular tree, which is better called the vascular net, is to convey blood to all parts of the body and return it to the heart. Blood is the peculiar tissue which from the times of primitive man has been recognized as having a truly vital significance to man and animals. Religious rites, including Hebraic, Christian, Egyptian, Maya, Aztec, to mention but a few, have included blood sacrifices. Anyone who has seen the great sacrificial stone in the National Museum at Mexico City, with its deeply cut channels to permit the sacrificial blood to be transported from the scene of sacrifice, can visualize the significant part that blood has played in the minds of men who would appease the gods by offering this magic tissue along with the heart, the organ which propels it.

Goethe profoundly summarizes the implications of vascular tissue when he has Mephistopheles say, "Blut ist ein ganz besonderer Saft," as Walters has pointed out in his excellent comparative text.

Presumably developed from body fluids somewhere in the invertebrate lineage, it has gradually taken on the functions of nourishment, of oxygen-carbon dioxide transport, of a phagocytic and bactericidal agent, and of a vitamin and hormone carrier. Blood is a liquid plasma carrying various formed elements or cells of specific types and with specific functions, as well as salts or electrolytic agents in solution.

The cells are of three general types, *erythrocytes*, or red blood cells; *leukocytes*, or white blood cells; and *thrombocytes*, or blood platelets (Fig. 212). These cells are formed in the red bone marrow, the spleen, and the lymphatic system.

Erythrocytes. The erythrocytes, or red cells, the most numerous of the blood cells, with the thrombocytes constitute the only cells which limit their work to the blood stream, since the white cells use the blood channels primarily as highways from the site of their formation to their destination in the body tissues. The red cells are biconcave discs, which

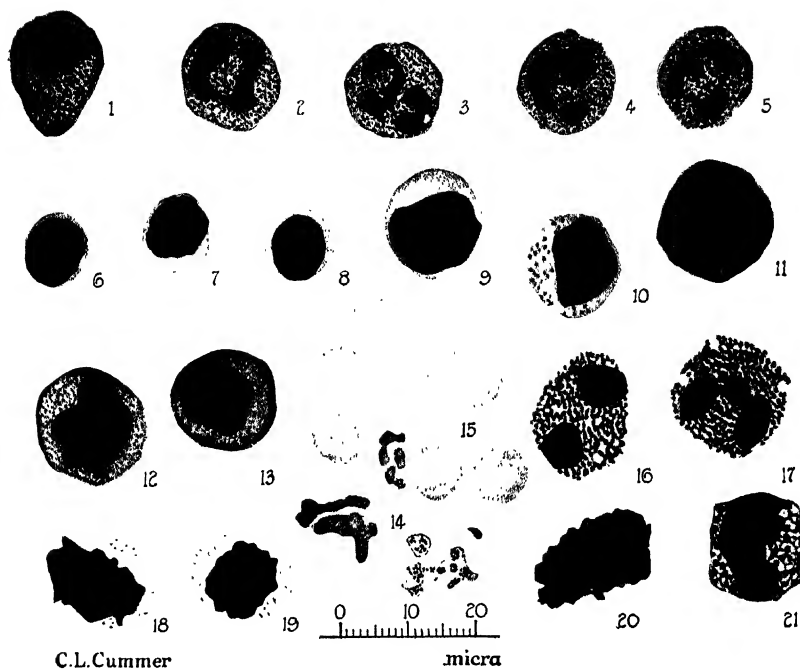


FIG. 212. Types of blood cells. A, erythrocytes; B, granulocytes; C, lymphocytes; D, monocytes; E, thrombocytes. (After Cummer, Courtesy of Lea and Febiger.)

in man and other mammals have an average diameter of 7.5 microns, although in the chevrotain they may be 2.1 and in the goat 3.6 microns. In the amphibian *Amphiuma*, better known as the hellbender, the diameter may be 75 microns, or ten times the above average. In their adult phase the mammalian red cells are anuclear, except in the camel, where the nucleus persists. In the human body there are about 25 trillion of these cells, and since their life span is 25 to 30 days, approximately 1 trillion are worn out and replaced daily. Newer techniques involving use of tracer substances modify these estimations somewhat; some red cells apparently may persist for as long as 120 days. The total mass of these packed cells in the blood is about 2,500 cc. The number per cubic millimeter is slightly larger in the male, averaging about 5,000,000, as compared with the female, 4,500,000. In the white rat there are about 7,000,000 red blood corpuscles per cubic millimeter in the female and 8,000,000 in the male; in the cat the values are about 8,500,000 for the female and 9,000,000 for the male. Haden states that about 60,000 may be placed on the head of a pin. These oxygen-carbon dioxide carriers are vitally necessary, since the plasma alone is unable to carry sufficient oxygen to nourish the tissue. In the red blood cells there is a concentration of about 34.2 per cent hemoglobin. The hemoglobin, a complex protein with iron attached to it, is the carrier of the oxygen and carbon dioxide.

The great value of hemoglobin to respiration is its great capacity for oxygen adsorption; a single gram will unite with 1.34 cc. of oxygen. This means that, if the body contains 5 l. of blood with a normal hemoglobin content of 770 gm., the total oxygen capacity of the blood is about 1,030 to 1,050 cc.

Chlorophyll, the protein plant pigment which is the essential agent in transforming inorganic to organic combinations, has a structure closely similar to that of hemoglobin. The chief difference is that the heme molecule contains iron, while the chlorophyll molecule contains manganese. This similarity of structure has led to attempts, some of which appear promising, to utilize chlorophyll in wound healing and as a growth stimulant to certain tissues.

Old cells die by fragmentation and become engulfed by reticulo-endothelial cells in the spleen and liver. The end product of this breakdown is bilirubin, which is utilized by the liver in the manufacture of bile.

Leukocytes. The leukocytes, or white blood cells, are of three distinct types, *granulocytes*, *lymphocytes*, and *monocytes* (Fig. 212). About all they have in common is their relatively colorless appearance in the unstained state.

Granulocytes. Granulocytes receive their name from the presence of numerous granules in the cytoplasm, which are revealed in properly stained blood smears. These granulocytes, again, are of three kinds based on their staining reactions. They may be neutrophilic, eosinophilic, or basophilic; in other words, they may show neutral, acid, or basic reactions. Aside from their granular cytoplasm the polymorphic nucleus is their outstanding feature. Granulocytes are motile and are able to penetrate tissues. In fact, their work is almost exclusively carried on in the tissues outside the blood. They are phagocytic, which means that they engulf and devour foreign or toxic agents; they have diameters of 7 to 9 microns; their life span is 3 to 4 days. They increase greatly in number during infections, a fact of value in medical diagnosis. The neutrophils comprise about 60 to 70 per cent, the eosinophils 2 to 4 per cent, the basophils 0.5 to 1.5 per cent of the total granulocyte count in the human body.

Lymphocytes. Lymphocytes, considerably smaller than granulocytes, average 4 to 6 microns in diameter. This relatively small size, plus the small amount of cytoplasm and large nucleus they contain, usually identifies them. In contrast to the red blood cells and the granulocytes, lymphocytes arise only in lymphoid tissue, *i.e.*, in the spleen and the lymph glands. These cells, in contrast to the granulocytes, are not phagocytic or motile. They are plentiful in mucosal tissue, at the site of wounds or infections, and in the lymph glands and spleen. While they may be increased in certain infections, comparatively little is known concerning their true functions. From 5 billion to 10 billion are formed daily in human blood; their span is less than 24 hours. About 20 to 30 per cent of the white blood cell count is made up of lymphocytes.

Monocytes. The monocyte is the remaining type of white blood cell. This is the largest of the blood cells, ranging from 12 to 20 microns in diameter. It constitutes 5 to 10 per cent of the white cell count. It is characterized by a large eccentric nucleus and a cytoplasm, dotted with fine, pinkish granules. It is actively phagocytic and may be formed both in bone marrow and spleen.

Thrombocytes. Thrombocytes (blood platelets) are the third distinctive type of blood cell (Fig. 212). They are small, clear bodies of 2 to 3 microns diameter. They take on a lilac color with Wright's blood stain and range from 200,000 to 400,000 per cubic millimeter of human blood. Their life span is about 304 days. They are necessary for blood clotting. The cells furnish prothrombin, which sets free thromboplastin and starts clot formation. The steps in this reaction presumably are these,

Prothrombin + calcium ion = thrombin and fibrinogen

which in turn forms the clot. The fibrinogen is formed by the action of thrombin. In hemophilia apparently this disintegration does not take place. This is a disease that affects the male, although the female is the carrier. It is marked by an inability to form or segregate the elements necessary for blood clotting. Individuals so afflicted are known as bleeders.

THE LYMPHATIC SYSTEM

The lymphatic system is functionally and structurally associated with the veins in returning fluid elements to the circulation (Fig. 213A). The fluid returned is lymph, a colorless derivation of the plasma, also known as tissue fluid, since it bathes the tissues and subsequently enters the lymph capillaries which lie in the tissue spaces. The tissue fluid presumably is derived from the blood by osmosis and diffusion, and the excess of this lymphatic fluid must find its way back to the circulation; this it does by the lymphatic channels. The permeability of the lymph capillaries makes possible this return. Bodily activity and massage increase the circulation of lymph, while rest and inactivity decrease it. The lymph contains the same protein and inorganic salt constituents as does blood plasma. It also contains lymphocytes in great numbers, but ordinarily red blood cells and blood platelets are absent or scanty.

Besides serving in the very necessary capacity of lymph carrier, the lymphatic system has other significant functions. One is to absorb digested fats through the lacteal vessels in the villi of the small intestine. This digested substance, known as chyle, is carried in a finely emulsified state from the lymphatics into the subclavian veins by the thoracic duct,

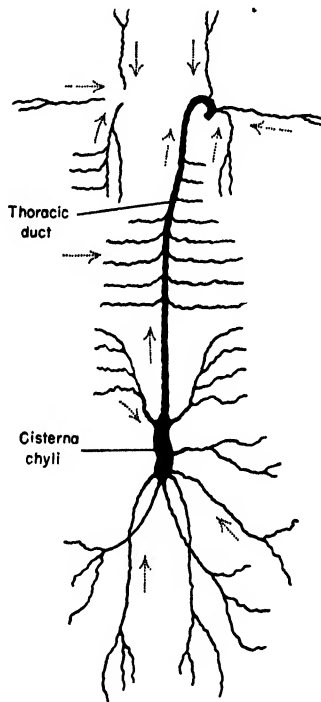
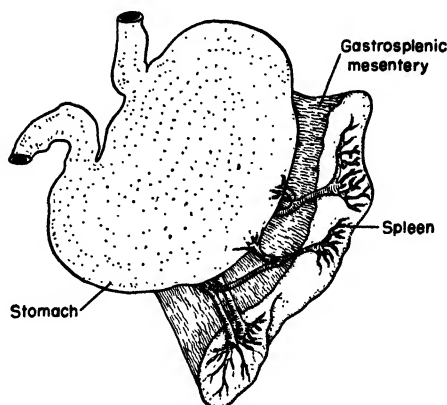
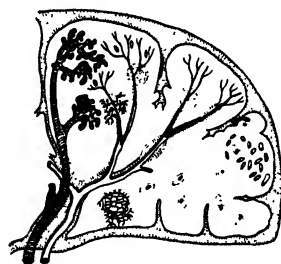


FIG. 213A. Lymphatic system. The lymphatic channels represent a one-way system opening into the subclavian veins. A chyle receptacle, the cisterna chyli is an expansion of the main lymph channel in the abdomen. It continues cephalad as the thoracic duct.

to be described (page 427). Another function is carried on by the lymph glands, or nodes, which interrupt the lymph vessels at various points. These glands are one source for the production of lymphocytes of the blood and probably also filter the lymph as it passes through the glands.



B



C

FIG. 213 B and C. Spleen. B, although in close proximity to the stomach, the spleen is functionally a part of the lymphatic-vascular system. C, in histological detail, it exhibits a white and red pulp mass, malpighian corpuscles, germinal centers, and a high degree of vascularity.

It will be recalled that the lymphocytes are one of the white blood corpuscle types, constituting in the human blood about 20 to 30 per cent of the white cell count.

Several additional features should be noted about the lymphatic network. It is a one-way system of capillaries and larger lymph vessels lined throughout by endothelial cells. It arises from the venous system, since ontogenetically its origin may be traced to lymph sacs developed

from endothelial-lined capillaries after their formation from the primitive internal jugular veins. From these sacs capillary networks spread over the body. Confluence and anastomosis of the larger elements in these plexuses form the larger lymphatic vessels. Permanent connections between the right and particularly the left jugular veins and the lymphatics are retained through the right lymphatic trunk and the thoracic duct, respectively.

The cisterna chyli, a large lymph-collecting reservoir at the level of the lumbar vertebrae (second in man), is derived embryonically from vein sprouts in the region of the wolffian bodies and receives connections from lymph sacs associated with the iliac veins. It also receives connection from the viscera of the pelvis and from stomach and intestine by way of the intestinal trunk. The cisterna chyli joins the thoracic duct, which eventually retains a connection only with the left jugular-subclavian confluence.

The lymph glands, or nodes, appear in the lymphatic capillary plexuses after the latter are well defined. Their exact mode of origin is in doubt. One view, since lymphocytes already circulate in the lymphatics before the glands, or nodes, are formed, is that the lymphocytes lodge at certain points of the plexus and become converted to lymph nodes at these sites. Another is that they arise as new structures *in situ*. Lymph glands have a connective tissue *capsule* surrounding the *cortex*, from which supporting *trabeculae* extend into the *medullary substance* of the gland. Inside the capsule, *lymph sinuses* immediately surround the trabeculae, and inside these is the *lymphoid tissue*, which in the cortical areas forms *germ centers*. *Afferent lymph vessels* penetrate the capsule. The lymph passes through the meshwork of the sinuses and lymphoid tissue and eventually is re-collected in the *efferent vessels* which leave the lymph node at the hilum. Lymphocytes originate in the germ centers.

The lymph glands, like the lymphatic plexuses, are arranged in superficial as well as in deep groups. The superficial glands of the lower extremity lie in the groin; those of the upper in the axilla. Others occur on the sides of the head and neck. Deep glands are associated with the pelvis, abdomen, generative organs, stomach, intestine, thorax, mediastinum, trachea, and larynx.

The distribution of lymphatic plexuses extends to most parts of the body, to the dermal layer of the skin, to the mucosa throughout the glands of digestion, excretion, and reproduction, to the lungs, and even to the tendinous ends of striated muscle. The skeleton, central nervous system, cornea of the eye, cartilage, and epidermis are not supplied with lymphatic vessels.

Lymphatic vessels are designated as of the first order when they arise in lymphatic capillaries and enter the lymph nodes. Such entering vessels are afferent. Their continuations beyond the nodes are efferent.

Lymph hearts, absent in human and mammalian lymphatic systems, occur as paired segmental structures in some of the caudate amphibians. In the tailless ones, paired inguinal and pectoral hearts appear as the propelling vessels for the lymph. These hearts are similar in position to the lymphatic sacs in the jugular and abdominal regions of mammals, from which the primary lymphatics originate. Valves are plentiful throughout the system. The amphibian lymphatics are of significance to the endocrinologist and obstetrician since it has been found that frogs lend themselves to pregnancy tests. Urine from the person to be tested may be injected into the frog's lymphatics.

The direction which the lymphatics of the various parts of the body take is of significance, particularly to the surgeon, since metastases follow the highways and byways of these channels. Cancer cells frequently break free from their primary loci, when they may be carried to distant glands and organs by these routes and establish secondary centers of malignant growth. Closure or failure of lymph channels to permit lymph circulation may result in edema. Elephantiasis, for example, results from obstruction of lymph passages of the lower extremities by the larvae of one of the Filariidae, the roundworm *Wuchereria bancrofti*.

THE SPLEEN

The spleen is a part of the lymphatic system (Fig. 213B). Embryonically it originates from the mesoderm and more particularly from a thickening in the dorsal mesogastrium. Thus it represents a derivative of the celomic epithelium. Eventually it is associated in position with the greater curvature of the stomach.

Its outer, or serous, coat is a peritoneal derivative joined with a dense fibroelastic capsule underneath. Trabeculae extend inward from this capsule, and in their anastomosing meshes are areolar spaces, which contain the splenic pulp. The trabeculae have smooth muscle fibers associated with them. This, together with the fibroelastic coat, makes considerable dilatation and contraction possible. The arterial supply is copious, terminating in small tufted arterioles in the splenic pulp. The latter, a fine network of fibers and flat, branching cells, is continuous with the trabeculae.

The blood passes into the splenic pulp and is re-collected in veins from the open sinuses. These veins unite into one or more large splenic veins, which emerge at the hilum and enter the portal circulation.

A spleen occurs in all jawed vertebrates but is absent in the cyclostomes. Essentially its structure is similar throughout the vertebrate series, although its position may vary from class to class. Its distinctive functions are not known. It may be removed without apparent harm; it furnishes new blood cells in fetal life; hormonal activity has been ascribed to it in connection with the control of blood platelet formation; it is believed by some to contain a nonaging factor supplied by its reticuloendothelial network; it is a blood reservoir. In life its size varies greatly, depending upon its blood content; it destroys red blood cells in the adult through its phagocytic reticuloendothelial system.

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CHAPTER 11

THE EXCRETORY AND REPRODUCTIVE SYSTEMS

THE EXCRETORY SYSTEM

Excretion denotes the removal of wastes from the animal cell or body. In biology the term is restricted to the process of the elimination of substances that have taken part in metabolic activities or that represent the breakdown products resulting from such activities, while the term *defecation* is employed for the removal of unabsorbed remains of digestion.

Excretion permits the organism to maintain itself at a specific level of physiological performance, which implies that it can tolerate a certain concentration of water and of solutes (salts and nitrogenous compounds of various types in solution) in the protoplasm or in the blood stream. Unless the animal possesses some mechanism for eliminating such solutes as they accumulate after any metabolic activity, the machinery breaks down and the life of the organism is shortly brought to a halt.

The function of an excretory system may be clarified by a crude comparison to the activities in a furnace when the fire is properly stoked. Given the right amount of air and coal, and assuming removal of the ashes as products of combustion, the ash concentration is kept at a minimum and does not reach levels which jeopardize the fire. Under these circumstances it may be maintained over prolonged periods. Retention of these oxidation products, on the other hand, is rapidly fatal to the fire.

EXCRETORY PRODUCTS

According to Howell, the excretory products which are thrown into the circulation for elimination are excessive water; inorganic salts; urea (CON_2H_4), a nitrogen compound, an amide of carbonic acid; purine bodies (uric acid, xanthine, hypoxanthine); creatinine; hippuric acid; oxalic acid (calcium oxalate); conjugated sulfates and glucuronates; aromatic oxyacids; urinary pigments; and sex hormones.

This bewildering list does not include all the products eliminated in health or disease. It emphasizes, however, the multitudinous energy reactions in the various tissues which end in these highly complex compounds and gives an indication of the problems which an excretory system must solve.

Nitrogen resulting from protein digestion is perhaps the most common agent eliminated. It occurs in several of the compounds listed above. Sulfur, also a common constituent, appears in sulfates and is eliminated. Water is lost constantly from the lungs, sweat glands, and kidneys. In the human being, for example, 300 to 3,500 cc. of water may be eliminated daily from the kidneys.

Inorganic salts, common constituents of urine, are taken in with the food, or they result from the breakdown of proteins or phosphates in the food.

EVOLUTION OF THE EXCRETORY SYSTEM

Not all of the above-indicated fractions are eliminated by all kidneys in the chordate series. Like the other organs, the kidneys have undergone a lengthy evolution both in invertebrates and vertebrates. In the former the following steps may be tabulated in their rise:

1. The contractile vacuole in Protozoa gathers and the cell membrane eliminates wastes. Apparently hydrogen ion concentration as well as the mechanical factor of size of the vacuole determines elimination of its contents.

2. Solenocyte or flame-cell or protonephridial systems consisting of capillaries terminating in ciliated tufts at one end and joining collecting tubules at the other remove water and wastes mechanically and by osmotic action. Such systems occur in flatworms.

3. Nephridial systems connecting the celom with the outside present tubules in close proximity to the vascular supply for elimination of wastes by osmosis in annelids.

4. Celom ducts from the celom to the outside serve as reproductive ducts.

In the chordate series the steps are as follows:

1. Protonephridia; restricted to Cephalochordata.

2. An archinephric system extending the length of the celom; the essential elements of such a system are segmental tubules opening into the celom and associated with the vascular system. An archinephric drainage duct opens into the cloaca. This type is typical of the myxinoids.

3. A pronephros, or head kidney; the first embryonic kidney of amniotes is partly functional in cyclostomes, in some bony and dipnoan fishes, and in the embryonic stages of many more.

4. A mesonephros, which is the functional kidney of anamniotes, *i.e.*, cyclostomes in part, fishes with the exceptions noted, and Amphibia.

5. A metanephros, or functional kidney of the amniotes, *i.e.*, reptiles, birds, and mammals.

Once the problems involved in excretion are clearly visualized, an understanding of the structures that constitute the various types of excretory systems and that solve these problems is not difficult. Required are semipermeable membranes, a vascular system or a circulating protoplasm, and a system of ducts for removal of wastes from the body. These by no means explain the physiochemical forces responsible for excretion, but they indicate a few of the essential structures that make the physiochemical changes possible.

We cannot here enter into a detailed description of various invertebrate systems except to state that the nephridium of the annelid has

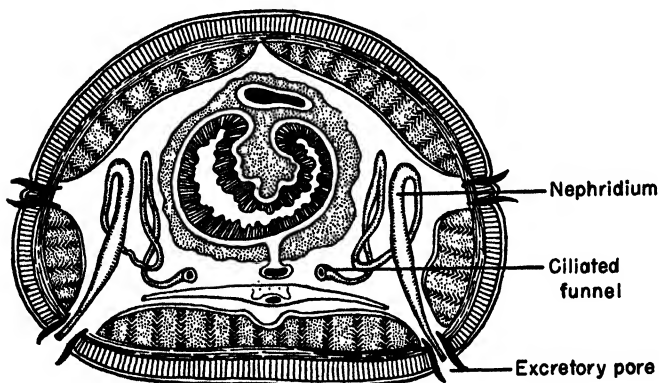


FIG. 214. The annelid nephridium. The earthworm has a ciliated funnel opening into the celom. The body of the nephridium is coiled and is in close communication with a blood vessel. The coil opens to the exterior by the excretory pore. Annelid nephridia are segmental.

essential structures similar to those of pro- and mesonephros (Fig. 214). This does not mean that it is homologous with them. The system has an opening into the celom; it is in close proximity to the blood stream; it has coiled tubes; and it opens to the outside.

Originally the chordate excretory system, it appears, consisted of paired segmental tubules extending the length of the celom, each opening into a longitudinal duct at one end and into the celom by a ciliated peritoneal funnel at the other. This was the so-called *archi-* or *holonephros*. Presumably the original function was to convey genital products to the outside; the true excretory function was secondary and acquired its highly refined functions more recently.

Essentially the paired tubules of pro- and mesonephros consist of a

ciliated peritoneal funnel, communicating with the celom, and a *tubule* proper, which expands into a widened chamber, called the *nephrocele*. Into the medial side of the nephrocele a *glomerulus*, or capillary knot, pushes, and the wall of the nephrocele cups about it to form the *Malpighian body*. Connecting nephrocele with the longitudinal duct are two additional specialized parts of the urinary unit, a *ciliated duct* and a *glandular tubule*.

The original organ, which presumably extended throughout the entire trunk, has been termed the archinephros, as has been indicated (Fig. 215). In the anamniotes this is no longer evident; instead, a certain few anterior tubules develop first (pronephros), followed by a similar development further posteriorly (mesonephros). In the amniotes the second group of tubules is succeeded by a third stage, further caudally, the metanephros. The myxinoids more nearly represent the ideal state of archinephric development than do any other animals.

To understand the source from which the tubules and their adnexa spring, it is necessary to consider their embryology. In the early stages of individual vertebrate development the mesoderm lateral to the dorsal midline divides into paired mesoblastic somites, evident in the lateral half of any appropriate embryo. These somites divide into dorsal segments, epimeres, below which are mesomeres (nephrotomes), the latter a fusion with the lateral plates (hypomeres) ventrally. The connection between nephrotome and epimere becomes lost, but an open communication between the epimere and the lateral plate, which meantime has exchanged with the celom, is retained as the nephrostome, and just beyond it the captured celom, the nephrocele, also persists. At the same time the evagination from the lateral wall of the nephrotome develops into a tubular tube. These tubular evaginations extend longitudinally, forming the longitudinal duct. This is the pronephric duct, which places the excretory tubules in communication with the venous system. More posterior tubules continue to use this channel as they develop.

In elasmobranchs; it is then called the mesonephric, or wolfian, A pronephros

cele may occur. There is a variable degree of development of the pronephros in chordates. It is partly functional in cyclostomes, as indicated in the lampreys.

In Amphibiae, the bony fishes, including Actinopterygii and Diptherostomi, and the limbless amphibian Apoda. In the remaining amniotes, including the reptiles, birds, and mammals it is strictly vestigial; it persists briefly during development, but with the exception of the pronephric duct, which is appropriated by the mesonephric tubules, it then disappears. Typically the pronephros is a system of paired segmental

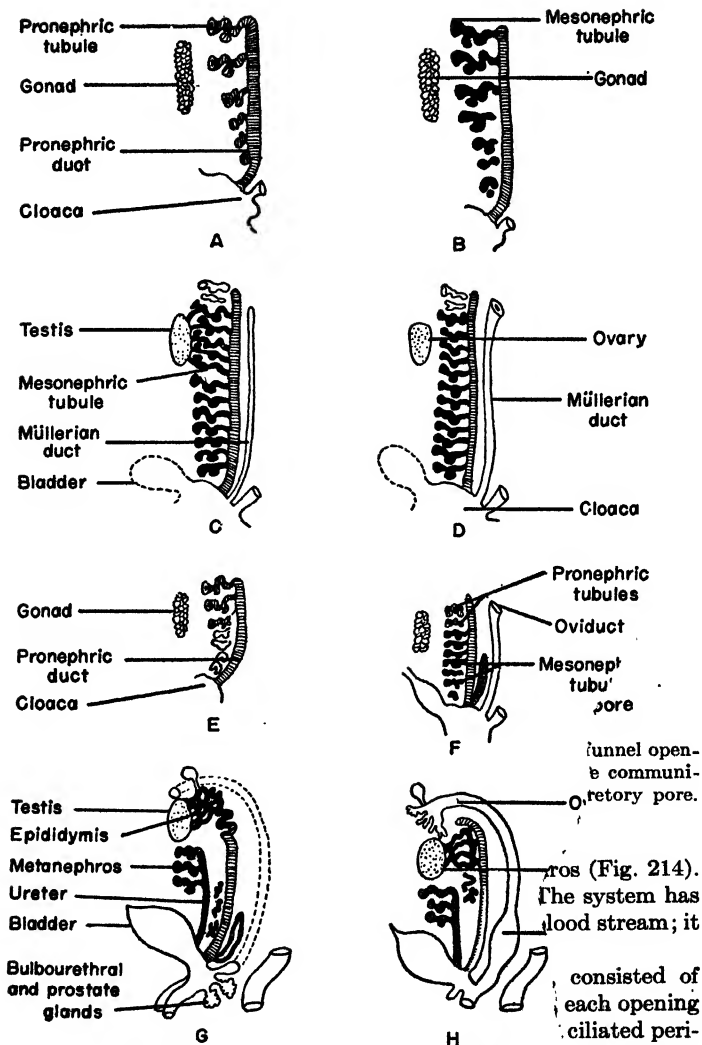


FIG. 215. Pronephros and Mesonephros. The pronephros differs from the mesonephros in position and in its relationships to gonads. It is segmental, each segment occupying one segment of the body. It opens to the exterior by a pair of tubules in each segment it occupies. A, B, pronephros in fish; C, mesonephros in male amphibian; D, mesonephros in female amphibian; E, pronephros in the fetal male and female amniote; F, mesonephros in the male and female fetal amniote; G, H, relations of urinary and reproductive systems in the adult male and female amniote. (After Wiesersheim.)

ducts leading dorsally from the celom to the longitudinal ducts that open into the cloaca. Between the celomic openings (peritoneal funnels) and the nephrocelostomes, as the openings of the excretory ducts into the longitudinal duct are called, is a variable development of glomeruli (blood vessel knots) and nephrocele. The cupping of the nephrocele wall about the glomerulus results in the formation of Bowman's capsule.

In animals with large-yolked eggs or without a free larval period, the pronephros is vestigial and short-lived; in those with brief embryonic development and long larval periods, it is functional. Further, its connections with the celom differ from class to class. In some, the peritoneal funnels become confluent, and the nephrocele becomes an extension of the celom, as in the Dipnoi; or the nephrocele may be completely closed off from the celom. Likewise the tubules may be reduced to one in some of the fishes, three in the Anura. According to Goodrich it is better differentiated in the Apoda, with eight pairs of fully developed tubules, than in any other land group.

In the cyclostomes the two suborders, Myxinoidea and Petromyzonidae, are distinguished by two different types of kidneys. In the Petromyzonidae some remnants of a pronephros are retained, with nephrostomata leading into the celom and with a few segmental glomeruli. The mesonephros, which constitutes most of the kidney, shows a fusion of the individual glomeruli; the mesonephric tubules lose their connection with the celom. In the myxinoids, on the other hand, a peculiar type of "head" kidney occurs in the anterior nephrogenic region, while more caudally the homologue of a promesonephric organ is formed. The latter is a single segmental system whose canals communicate with the celom and open into the pericardial cavity by its nephrostomata and its tubules; the latter become branched and intermingled and surrounded by a rich vascular supply. Those pronephric ducts closely associated with a diverticulum of the cardinal vein communicate directly with this vein.

In elasmobranchs the organ more closely resembles an opisthonephros. A pronephros with three to seven tubules and a well-developed nephrocele may occur. A mechanical filtering rather than a chemical excretory function is assigned to it.

In Amphibia the pronephros varies from one, with three tubules, in the Anura, to one with at least 13 pairs in Geophis, associated with glomeruli as well as with coiled glandular tubules. Urodeles and Anura possess during their larval development a functioning pronephros, although as indicated it is reduced to two or three functional canals.

In reptiles the pronephros has almost disappeared, although in the

lizards, turtles, and crocodiles several pronephric tubules are laid down and are briefly functional. In birds and mammals the pronephros is entirely vestigial and without function. In man it has seven pronephric tubules but is without glomeruli. In the human embryo it appears in the region of the fifth cervical to the third thoracic segments but disappears by the time the embryo reaches a length of 4 mm.

Mesonephros. The mesonephros, like the pronephros, is a mesodermal derivative. Mesomeres (nephrotomes) caudal to those responsible for pronephros proliferation are laid down when the latter begins to disappear (Fig. 215). It will be recalled that the mesonephric tubules utilize the pronephric duct, now called the wolffian, or mesonephric, duct. Segmental ducts, the functional elements of the mesonephric system, open into the celom. Above this opening the glomerulus pushes into the medial side of the expanded canal, while the dorsolateral extension of the tubule joins the mesonephric duct. Essentially, therefore, there is no structural difference between pronephros and mesonephros at this stage. Continued development of new, secondary mesonephric tubules obscures the original segmental nature of the system. This combined with closure of many of the peritoneal funnels brings about a condition roughly comparable with that observed in the metanephros. In birds and mammals the peritoneal funnels do not open except at the anterior end of the mesonephros, where they function as sperm ducts. In the anamniotes, where the mesonephros functions as the adult kidney, there is nevertheless a tendency for the anterior part of the organ to become vestigial. In the fishes this may be converted into a lymphoid organ—in life a dark, highly vascular mass, anterior to the functioning kidney. The posterior part of the mesonephros, on the other hand, tends to differentiate further by acquisition of the independent aortic blood supply. This has given rise to the designation opisthonephros by Kerr.

In the human embryo the mesonephros, like the pronephros, is transitory. It appears in the region of the sixth cervical to the third lumbar segments as a series of segmental tubules, one end of which opens into the mesonephric duct; the other, which does not open, surrounds the glomerulus, a tuft of blood vessels. The mesonephros, with the exception of the mesonephric duct in the male, which takes on a reproductive function, largely disappears by the fourth month of fetal development. The elements retained in the human male form the epididymis, ductus deferens, seminal vesicles (secondary diverticula from the caudal portion of the mesonephric ducts), and the ejaculatory duct, which joins the urethra at the base of the bladder.

The reproductive role of the mesonephric duct should not be lost sight of. According to Goodrich, the original function of the segmental

tubules was probably to convey spermatozoa and ova to the outside, and he considers the male genital ducts as continuing this function. Since the testes are not in direct communication with the celom, except in the cyclostomes, a system of ducts is necessary to convey the spermatozoa to the exterior. This is effected by *vasa efferentia*, which lead from the *testes* to the *mesonephric tubules*; the latter open into the *mesonephric duct*, which in turn terminates in the *cloaca*. A varying number of *vasa*

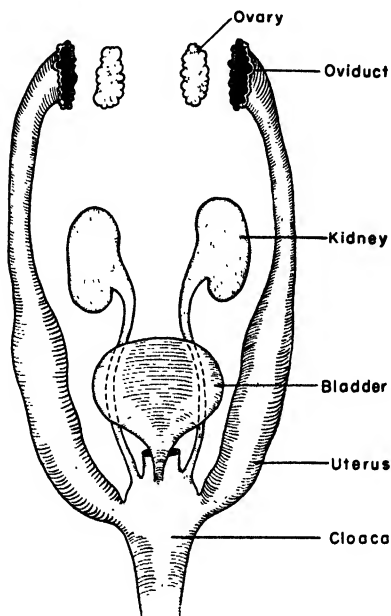


FIG. 216. Relation of the urinary bladder to the excretory system. In reptiles and birds the bladder opens into the cloaca; in mammals it leads into the urethra.

efferentia are associated with the anterior end of the mesonephros, which then tends to lose its excretory functions. In *Polypterus*, testis and mesonephros are independent, the former sending its products directly to the cloaca by a *vas deferens* that has no communications with the mesonephric tubules.

Bladder. Associated with the excretory functions above the levels of the fish, with the exception of birds, is a urinary bladder (Fig. 216). This may originate as an evagination from the cloaca, either from the dorsal or ventral wall, or it may arise as an allantoic outgrowth. The

latter is the embryonic respiratory organ of amniotes. Another mode of origin of the bladder is the fusion of the posterior ends of the urinary or wolffian ducts. Below the mammalian level the mesonephric ducts or ureters open into the cloaca, and the urine passes secondarily into the bladder. With the disappearance of the cloaca in mammals, the ureters open directly into the bladder, whence urine is carried by the urethra to the urogenital canal and thence to the exterior. In a strict sense the urethra is the short canal leading from the bladder to the junction with the common carrier for urinary and genital products in the mammalian male. In the female the two products are carried by separate ducts.

Metanephros. The metanephros departs from the meso- and pronephros so far as its origin is concerned. It is twofold in origin; one part, destined to form glomeruli, Bowman's capsules, proximal tubules, Henle's loops, and distal convoluted tubules, arises from two bands of nephrogenous tissue which extend caudad from the mesonephros. The other part, largely tubular, arises as a pair of diverticula from the posterior ends of the mesonephric ducts where they join the cloaca.

These diverticula, representing the future ureters, grow craniad into the nephrogenous mass. In that mass they expand into the pelvis and calyces of the kidney, while further extensions, the collecting tubules, join the secretory tubules (distal convoluted tubules), formed *in situ* in the nephrogenous tissue. As indicated, glomeruli, Bowman's capsules, and secretory tubules are formed in the metanephros proper. It will be observed that the metanephric tubules do not open into the mesonephric ducts; that the metanephros is not a segmental organ; and that it never has peritoneal funnels permitting direct communication with the celom.

In the human embryo the bladder is an outgrowth of the cloaca and of the termini of the mesonephric ducts.

The differences in the metanephros of the amniotes are of a minor and secondary nature. In the reptiles and the birds the kidney lies quite caudally in the abdominal cavity. It is extraperitoneal, as it is in all amniotes. In the snakes it takes on a unique appearance owing to its tandem arrangement, an expression of inner stream lining which reflects that of the body form. It has a lobulated appearance, but its functional units are typically metanephric. Even though a cloaca is retained in the reptiles, a urinary bladder is present. In this case the ureters open into the cloaca, and the bladder receives the urine secondarily from this source. In birds the kidney is usually three-lobed, each of the three lobes seated in fossae of the ilium. A bladder is not developed in the adult bird, and urinary products are carried into the urodeum, a division of the cloaca, and thence to the exterior.

The Mammalian Kidney. The mammalian type of metanephros falls into several distinct patterns, depending upon the number and the arrangement of the papillae that mark the terminations of the various collecting tubules. The simplest of these has but one papilla marking the openings of the collecting tubules into the pelvis of the kidney. This is typical of the monotreme, marsupial, and insectivore metanephros; in a second, a series of collecting tubules open into the kidney pelvis without definite papillae. This is representative of artiodactyls and carnivores. A third type found in primates and in the pigs might be derived from combining the collecting tubules of the second type into several papillae and calyces. In Cetacea and in cattle, further division of the ureter results in a series of renuli, or lobules, each comparable to a kidney with a single lobule.

The mammalian kidney is bean-shaped, about 4 to 4½ in. in length in man, 2 to 2.5 in. in breadth, and about 1 in. in thickness (Fig. 217). A single gland weighs 110 to 180 gm. Laterally, each kidney has a convex border. Medially, it has a concavity, at the center of which is a deep fissure, the *hilum*. Renal vessels including arteries and veins, ureter and nerves find entry by way of the hilum. A connective-tissue capsule, the renal fascia, surrounds the organ and also encloses a considerable mass of fatty tissue, most plentiful about the hilum and the poles. The entire structure, as indicated, is extraperitoneal. The right kidney lies somewhat below the level of the left in a number of mammals, and each kidney is capped by an adrenal gland, the latter with endocrine functions. Closely covering the kidney substance a tightly fitting *fibrous tunic* continues as the lining of the *renal sinus*, the latter revealed upon longitudinal sectioning of the gland.

The *sinus* is the internal space of the kidney opposite the hilum. Its walls are the kidney substance, and the floor presents irregularities offered by the *renal papillae*. The last are conical elevations in the sinus surrounded by depressed areas into which vessels and nerves enter. It will be recalled that the ureters develop into the pelvis upon their approach to the kidney substance. These funnel-shaped expansions extend into the sinus. In the sinus also the pelvis separates into two or three major *calyces*, the latter subdividing in turn into six to eight minor ones. The last expand funnel-like as they approach the sinus floor, where their margins enclose the renal papillae. Smooth muscle fibers surround these calyces and exert a milking action on the tubes, thus aiding in expressing urine into the pelvis.

A longitudinal kidney section reveals an internal *medullary* and an external *cortical portion*. Most conspicuous in the medulla are 8 to 16

renal pyramids, whose bases mark the outer limits of the medullary substance. Two or three pyramids frequently terminate in a single papilla.

The cortex, more granular in character than the medulla, not only covers the bases of the renal pyramids, where it forms *cortical arches*, but extends between them toward the renal sinus. These extensions are the renal columns, known as the *columns of Bertin*.

The functional and structural unit of the kidney, the *nephron*, includes Bowman's capsule and glomerulus, a proximal convoluted tubule, Henle's

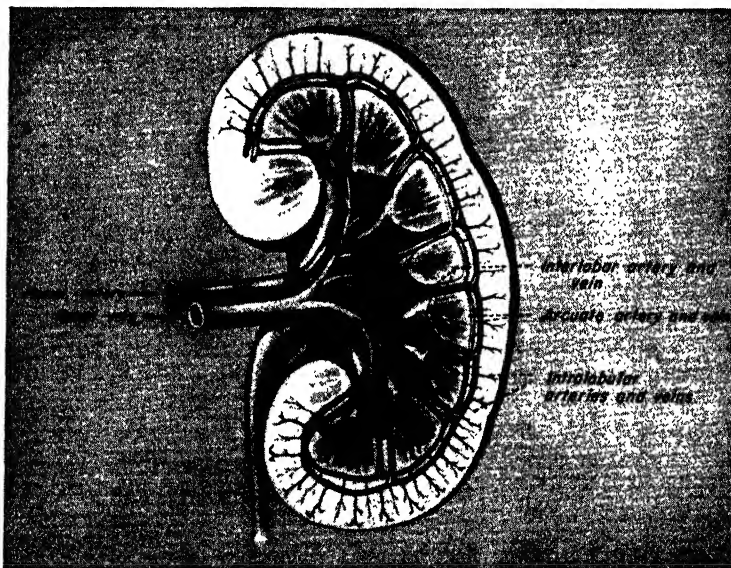


FIG. 217. The adult kidney in section. (Courtesy of Sharp and Dohme.)

loop, and a distal convoluted tubule (Fig. 218). There are about 1,250,000 of these units in each human kidney. The *tubule* begins in the cortex in Bowman's capsule surrounding a *glomerulus*, the microscopic capillary knot. An afferent arteriole, which breaks up into capillary loops within Bowman's capsule, sends the blood in; an efferent arteriole carries it away from the capsule. The total capillary surface of all glomeruli amounts to about 1 sq.m. Bowman's capsule is made up of flattened epithelial cells. Beyond the capsule is the *proximal convoluted* portion of the *tubule*. As it approaches the base of the medullary pyramid, it makes a sharp U bend and returns as the *ascending arm* of

Henle's loop, much thicker than the descending arm. Reaching the cortex, it forms the *distal convoluted tubule* and opens into the *straight collecting tubule*. Ascending loops and straight collecting tubules traverse the *medullary rays* of the cortex, while the excretory tubules, which represent the confluence of several *straight collecting tubules*, pass to the apex of the papilla, where 8 to 18 open into a *minor calyx*.

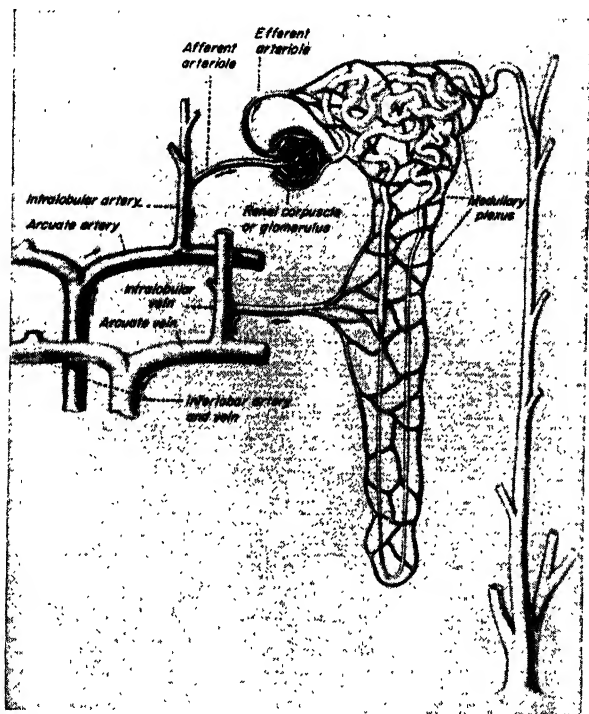


FIG. 218. The nephron. The unit of function in the metanephros is the nephron. Its various parts carry on highly specific activities. The units open into collecting tubules, and the urine passes from these into the hilum of the kidney thence to the ureter and into the bladder. (Courtesy of Sharp and Dohme.)

Since kidney function depends upon the integrity of the blood stream, its relationship to the gland should be understood. Direct branches from the abdominal aorta, the renal arteries, pass into the hilum of the kidney. These arteries commonly fork into an anterior and a posterior branch before entering the organ. Each of these branches supplies its

respective portion of kidney. Interlobar branches pass between the pyramids, at whose bases they form arches designated as arcuate arteries. These last give rise to small vertical interlobular arteries, which ascend through the cortex toward the periphery of the kidney. The interlobular arteries terminate generally in afferent glomerular arterioles. The circulation to the proximal convoluted tubules, Henle's loop, and the distal convoluted tubules is derived from the efferent glomerular vessels. These vessels terminate in plexuses about the tubules, and the blood is collected in venous capillaries and thence into interlobular veins, arcuate veins, and interlobular and renal veins, thus reversing the pattern of the arteries.

Innervation is through tributaries from the celiac ganglion, splanchnic nerves, and aortic plexuses, which, after first forming a renal plexus on the renal vein leading to each kidney, send 12 to 20 small nerve fibers into the kidney. The innervation follows the arterial supply and consists of sympathetic elements as well as parasympathetic, the latter contributed by the vagus nerve.

THE REPRODUCTIVE SYSTEM

Reproductive Functions

Some mode of reproduction is required for the maintenance of every species. It is the one way in which the animal may achieve some form of permanence. It is a necessary phenomenon concomitant with individual life, unless we are willing to assume repeated new creations of similar forms. While sex was not and is not necessary for the reproduction of many animals and plants, Nature, nevertheless, found it expedient to divide (or simply happened upon the scheme of dividing) many flora and fauna into males and females. Whether this was initially but another manifestation of the division of labor which had appeared much earlier at simple metazoan levels, whether it was a series of chance mutations without meaning, or whether it conferred such marked advantages on certain groups that their monoecious ancestral types died out when confronted with this new two-faced competition it is difficult to state.

Of late it has been necessary to return to a very open-minded view concerning sex, when confronted with the experiments in parthenogenetic reproduction in the rabbit as carried on by Pincus. He, for example, has been able to induce cell division, growth, and complete development of the ovum within the uterus of a rabbit, merely by subjecting the genital tract and the ovary to cold. The results of this experiment should give any male pause. He may take comfort from the fact, however, that

lactation may be induced in the male mammal, including the human being, by injection of the proper pituitary hormone. Hence, if his role in one phase of the reproductive function is discontinued, he may still be of use in the nurture of progeny, the result of reproduction, provided that he continues to be born.

In the simplest dioecious reproductive mechanisms, by which we refer to the single-sexed male or female state, Nature did not concern herself with secondary organs of reproduction but focused on the production of germ cells. The starfish, while not a simple animal, nevertheless illustrates this streamlining, or concentration on essentials; ova or testes occur at the bases of the five rays and open directly to the exterior.

Such a system makes demands on the surrounding medium, either salt or fresh water. The water becomes the carrier and the breeder of the eggs, and agents or secretions accompanying that discharge of eggs must also serve as stimuli for the discharge of sperm or spawn.

Many fish did not go far beyond this reproductive level, although generally paired elongate canals carry eggs or sperm into the water. Again we must assume excitory elements passed out with the eggs which stimulate olfactory tracts or act directly on the male reproductive system to induce spawning. Casting their bread, as it were, on the water in this manner, while it yields returns, does demand large supplies of bread. Fish-roe and caviar eaters and observers of the egg-laying activities of frogs know that fish and Amphibia are richly endowed in this respect. Energy and food cost to maintain this method of reproduction is great. Nothing is wasted, however, and what is not developed into young fish or tadpole is eaten, or if the harvest of young is particularly plentiful these serve equally well as food. Thus establishing delicate balances, one species serves another directly or indirectly.

Some fish have broken this chain and made advances in reproduction far beyond what we might expect at their level. Internal fertilization and internal development in the many elasmobranchs has with one step changed conditions so markedly that instead of laying millions of eggs they number them by the dozen or less. Further, these large-yolked eggs, by tarrying in the uterus, are transformed into young sharks, which gives these fishes a more assured immediate future. To emerge from a womb with sufficient size, speed, and protection through tough skin, teeth, and sensory organs to ward off potential enemies confers an advantage; witness their success in maintaining their kind in spite of relatively few progeny.

Our knowledge of many features of reproduction is still meager. To this day the Arunta, Australian aborigines, do not associate copulation

with its frequent successful results, nor do we take much note of the role of eye, olfactory organ, ear, tactile senses, food, climate, or season in the reproductive activities beyond assigning some role to these various agents. To compensate for this lack of knowledge, no demand is made in most species for conscious knowledge of the nature of reproduction to assure its occurrence. Temperature, season, condition of the body, chemical agents, sensory organs combine to call forth sexual urges in animals. It remains to determine some of the patterns into which the reproductive system of the representative chordate classes has evolved.

Comparative Anatomy

Amphioxus. The male and the female chordate reproductive systems may be referred to two common patterns which apply to all chordate classes. These in turn possess many homologous parts and arise embryonically from similar structures. If all chordates are of ultimate common descent from an Amphioxus-like protochordate or from a cyclostome-like chordate, we should expect a fundamental similarity of architecture in the two sexes. Evidence leads more and more away from the view that an Amphioxus-like group was the progenitor of succeeding classes. The reproductive system is atypical in many respects in comparison with other groups. Thus there are a large number of paired gonads in both sexes; further, these are without genital ducts, and ova and sperm are discharged into the atrium and escape from the body by the atriopore.

Ovaries or testes are clearly discernible in the adult Amphioxus since they occur at the lower margin of the myotomes and appear as rounded, well-defined bodies (Fig. 16). They first appear in the floor of the myotome as a single cell in each myotomic pouch. Through proliferation they join the myosepta. The ripe male gonad consists of a sac-like germinal epithelium, a vascular envelope, by virtue of association with the cardinal vein, a connective-tissue attachment to the myotome, and a surrounding layer covering the vascular sac and the epithelium of the genital chamber. Spermatogonia are derived from the germinal epithelium and ultimately completely fill the germinal cavity.

The ovary distinguishes itself chiefly from the testes even in early differentiation by larger and fewer germinal cells. Ova and sperm are discharged by muscle contractions that rupture ovary and testes and send their products into the branchial pouches.

Spermatozoa are relatively smaller than are those of the Vertebrata; ova are characterized by relatively large amounts of yolk and by numerous vacuoles. The eggs are liberated through the atriopore, and

fertilization is external. The unique feature of the reproductive organs of *Amphioxus* is its segmental nature, pointing to a possible annelid-like background. On the other hand, Neidert and Leiber, who made an investigation of excretory functions of the *Amphioxus* gonad, homologize the pronephros (holonephros) of the Elasmobranchii with the gonads of the Acrania.

Tunicates. In the tunicates, in which a definitive excretory system is lacking and only excretory cells occur (*Salpa*), there is a specialization of individuals into oözooids, without sexual organs, and into blastozooids. The latter are protogynic hermaphrodites and are derived from the oözooids. The term *protogynic hermaphrodites* denotes individuals which first function as females and later as males. The oözooid, from which the blastozooid arises, possesses a stoloprolifer (germinal organ), from which the blastozooids develop as buds. The stoloprolifer arises ventrally near the posterior end of the endostyle. The blastozooids usually possess one testis and one ovary with the latter ripening first. The testis is a series of blind anastomosing channels; the ovary has a variable series of germinal cells. A vas deferens leads from the testis to the cloaca, and an oviduct likewise connects the ovary with that outlet. The oviduct is a channel for the spermatozoa that enter from another blastozooid. After fertilization the ovum is retained in the brood chamber; only a single embryo develops at a time. When it hatches, it develops into an oözooid. The young blastozooids are the gregarious, colonial sexual generation; the oözooids, or solitary forms, represent the asexual. This is an instance of alternation of generations, an unusual condition in the chordates.

Hemichordata. In the Hemichordata, that group of worm-like half chordates far removed structurally from the remaining Protochordata, the sexes are separate. The reproductive organs are segmental saccular structures extending dorsally to the pharynx and opening directly to the outside by a number of pores. In contrast to the peculiar conditions observed in the tunicates, fertilization is external. In some species of *Enteropneusta*, one of the hemichordate classes, an elaborate metamorphosis, reminiscent of the echinoderms, takes place. This involves development of a ciliated adult form. In other species of this class, development is direct. In the other class, the *Pterobranchia*, also exhibiting direct development, bud and zooid formation occurs.

In comparison with the reproductive system of the true Chordata, it will be observed that the above-described groups vary greatly and it would be difficult to derive, on the basis of their reproductive organs, the evolution of the Chordata from any of these classes. The segmental

nature of the system, production of buds or zooids, colonial habits of many representatives—all speak against such origin. When we examine the cyclostomes, however, we find greater similarity with the remaining chordates and better evidence for the possible evolution of the reproductive system from this class.

Cyclostomes. Of the cyclostomes, the Myxinoidea are hermaphroditic, but spermatozoa and ova do not ripen at the same time. The gonad, an elongate organ supported by mesenterial tissue, extends along the right side of the body cavity. The anterior end of this organ has been called the mesovarium, since it contains ova in various stages of ripening. The posterior portion, which contains ripening spermatozoa, has been termed the mesorchium. Younger animals apparently are predominantly male; older ones predominantly female. Eggs are enclosed in a tough shell when laid, and numerous holdfasts assure their attachment to seaweeds.

The gonads of the Petromyzonidae are unpaired; the sexes are separate. The ovary surrounds the intestine, and as egg development proceeds, the large-yolked, elliptical eggs, attached by connective-tissue fibers to the mesenteries, crowd the body cavity. No ducts comparable with mesonephric or müllerian ducts are developed, and the genital products when ripe are discharged into the body cavity and thence by abdominal pores to the urogenital sinus and the exterior.

Fishes. The elasmobranchs, which it will be recalled include such forms as sharks, torpedoes, and rays, show striking differences amongst themselves in the mode of reproduction, since in some species fertilization and embryonic development are internal, while in others the eggs are laid after receiving a tough outer shell.

Both ovaries and testes lie far forward in the body (Fig. 219A, B). The ovaries, dorsal to the anterior portion of the liver, are attached to the body wall dorsally, each through a mesenterial envelope, the *mesovarium*. In mature specimens the eggs are large, owing to the great amount of yolk. Eggs an inch in diameter are not unusual in the dogfish. The *ostium* of the oviducts lies ventral to the anterior end of the liver. The two *oviducts* have fused with the falciform ligament of the liver. The ostium thus presents a wide, funnel-like opening in the ventral part of the abdominal cavity. The ripe ova in close proximity to this opening are apparently captured or drawn in. The oviducts curve around the rostral end of the liver and extend posteriorly toward the cloaca. In mature specimens, a *nidamental gland*, a thickening in the anterior third of the oviduct, secretes the outer covering for the egg. In those species where development is internal only a thin membrane is

secreted by the gland; in others it is a tough membranous secretion with tendrils extending from the four corners of the pillow-like case, which act as holdfasts during embryonic growth.

The *uterus*, supported by the *mesotubarium*, represents an expanded portion of the oviducts, posterior to the *shell gland*. It is to be remem-

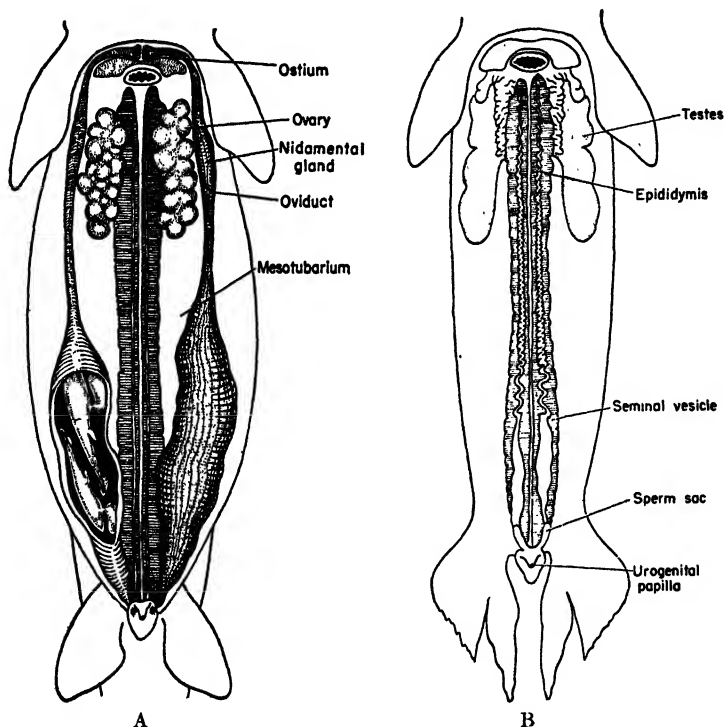


FIG. 219A and B. The elasmobranch male and female reproductive systems. Ovaries and testes lie far cranially in the body cavity. They are supported by mesenteries. Ova and testes pass their products into the cloaca.

bered that each oviduct has this uterine expansion. A pregnant shark may in this manner develop 4 to 12 and perhaps more young in a single pregnancy. The uteri, or oviducts, terminate one on each side into the *cloaca*.

In the male the testes are similarly located, as are the ovaries in the female. Each is supported by a mesenterial fold, the *mesorchium*. Carrying the products from the testes are a number of *mesonephric*

tubules which lead into the anterior end of the mesonephric duct. The ductules connecting testes and mesonephric duct form the *epididymis*. The mesonephric duct on each side, which now functions as a sperm duct, becomes greatly coiled and, as the epididymis, descends caudally over the ventral surface of the kidney. It expands near its posterior terminus into a *seminal vesicle*, which is further extended near its caudal end into a *sperm sac*. The latter represents an evagination of the duct extending ventrad and cranial from the seminal vesicle. The sperm sacs from the two sides unite in a *urogenital sinus* which opens at the tip of a *urogenital papilla* in the *cloaca*. In some selachian species, accessory reproductive organs, known as *claspers*, and representing finger-like extensions of the metapterygia, project along the medial sides of the pelvic fins. In copulation they are inserted into the cloaca of the female, and sperm traverses their grooved inner margins to reach the oviducts.

Urinary products are carried from the male dogfish kidney by a series of *accessory urinary ducts*, since the original mesonephric duct has been appropriated by the reproductive system. In the female this is not the case, and while secondary accessory ducts are present, a primary duct continues to function as a urinary channel. The *müllerian duct* (oviduct) in elasmobranchs arises from the longitudinal splitting of the pronephric duct.

The ganoid and bony fishes in a number of points depart from the selachian pattern. In the Dipnoi and ganoids the testis is elongate, extending dorsally in the abdominal cavity, filling the cavity in the ripened state. A comparison of the ganoid, dipnoan, and teleost fishes shows a gradual separation of testes and kidney through a loss of the vasa efferentia and epididymal duct and the appearance of a secondary ductus deferens so that the eventual outcome is a genital duct independent of the mesonephric duct. A urogenital sinus is formed cranial to the urinary bladder by the confluence of this secondary genital duct with the urethra. The bladder in those fishes where it occurs represents a fusion and expansion of the terminal parts of the mesonephric ducts.

The female reproductive system of Dipnoi and ganoids does not differ markedly from that of the elasmobranchs. In some ganoids, however, the ovary is a closed, sac-like structure, extended caudally into an oviduct that opens into the urogenital sinus. In these instances, the original ostium and oviduct have disappeared. This is also the usual condition in the teleost fishes.

Amphibia. Amphibian reproductive systems resemble those of the elasmobranchs more closely than those of the bony fishes. This relates particularly to the oviduct.

The ovary is a sac-like organ suspended from the dorsal body wall by a mesentery, the mesovarium. The oviducts, which have no direct connection with the ovary, extend forward almost to the base of the lungs and open by an ostium on the ventral floor of the abdominal cavity. The glandular walls of the oviduct secrete the albuminous-gelatinous substance around the egg. Posteriorly they open separately into the cloaca. In the *Anura* the caudal portions of the oviducts, before they enter the cloaca, are expanded into thin-walled uteri in which the eggs may collect before being laid.

Amphibian testes are small, white ovoid organs each suspended by a mesorchium from the dorsal body wall. The anterior portion of the mesonephric duct carries the genital products into the cloaca. The connection between the duct and the testis is effected by several genital ductules joined in a network in the testis, the rete testis. This rete testis communicates with the ampulla, which in turn forms the functional tubules. The pathways leading from the adult testis to the mesonephric duct are tubuli (where the spermatozoa are formed), rete testis, genital ductules or vasa efferentia, and mesonephric ducts. The latter open into the cloaca.

The gonads of anuran *Amphibia*, both male and female, are characterized by the presence of fat bodies, numerous finger-like pads of fat at the anterior ends of the genital organs. Apparently this food reserve is utilized in the formation of ova and sperm or in connection with the hibernating habits of the class.

Bidder's organ, characteristic of some *Anura*, occurs both in males and females and apparently represents a rudimentary ovary, since if the animal is castrated, this organ develops into a normal ovary. In young males, sex reversal may be brought about by early castration, which is then followed by development of the organ into an ovary.

It will be remembered that *Amphibia* have given up their gills for lungs, but in their development they still depend upon an aquatic environment. They, like the cyclostomes and fishes, are anamniotes. The amnion characteristic of the classes above the *Amphibia* has freed the developing embryo from many of the hazards that face its anamniotic relatives. While here and there fish circumvented the dangers that accompany development by permitting the embryo to linger in the uterus of the mother, it remained for the reptiles to introduce a new invention, the amnion. This carried with it consequences as profound in many ways as did the later introduction of the warm-blooded condition in birds and mammals.

We may consider these two introductions as great stepping stones in

vertebrate organizations, comparable in significance with the evolution of lungs: the amnion freed the organism from ocean, stream, and pond and captured, as it were, tiny fractions of these waters and restricted them about the embryo; warm-bloodedness, the other great advance, freed the animal from another restriction or barrier to life, namely, temperatures too low for cold-blooded groups to function.

In spite of the fact that this new device, the amnion, was introduced with the reptiles, the actual organs of reproduction show little modification from the pattern observed in the selachians and the amphibians.

Reptiles. In the turtle the female reproductive system includes paired ovaries and their oviducts, the müllerian ducts, and a clitoris associated with the cloaca. The ovaries are irregular bodies placed about midway in the abdominal cavity of the lizards and more caudally in turtles and Crocodilia. Since reptilian eggs are large, the ovaries when filled with ripe eggs crowd the pleuroperitoneal space. The oviducts are relatively short, and their ostia open separately, the entire tube supported by a mesovarium that in the lizards may aptly be called the broad ligament. The coiling of the oviducts observed in the amphibians also appears in many reptiles. In the snakes the oviduct is an elongate tube that in the ovoviviparous species is expanded into a thin-walled uterus. Caudally each oviduct opens into the cloaca. The eggs in most species are hatched outside the body and are covered by a tough capsule which may be partly calcified. The albuminous layer immediately surrounding the yolk is secreted in the upper portion of the duct, while the yolk containing the germ cell is the product of the ovary.

The clitoris in the female turtle is the homologue of the penis, or copulatory organ of the male. It is represented by a thickening in the ventral cloacal wall. No function has been assigned to it in the reptiles, although it contains erectile tissue.

The reptilian male reproductive organs are paired testes in close association with the ventral surface of the metanephridia, to which they are attached by the mesorchium; efferent ductules leading from testis to the mesonephric ducts (epididymis); and a penis. The epididymal, or mesonephric, ducts open into the ventral portion of the cloaca, for in both sexes the cloaca has become partly separated by a transverse fold into a dorsal proctodeum and a ventral urodeum. The intestine opens into the dorsal portion; ureters and genital ducts into the ventral moiety. In addition, a urinary bladder, evaginated from the ventral cloacal wall, extends cephalad from its cloacal junction. The penis in the Chelonia and Crocodilia is represented by a pair of longitudinal folds on the cloacal floor, between which is a groove. When the two folds become engorged with blood, their medial margins meet and complete a temporary genital

canal. The walls are cavernous erectile tissue that continues to their free termini, where a glans penis is specialized. Their bases are expanded into urethral bulbs. Underlying the floor of the groove is a fibrous body. This has paired penial retractor muscles attached to its under surface. Another type of copulatory organ, the hemipenis, appears in the lizards. The hemipenes are elongate, sac-like bodies extending caudally from the

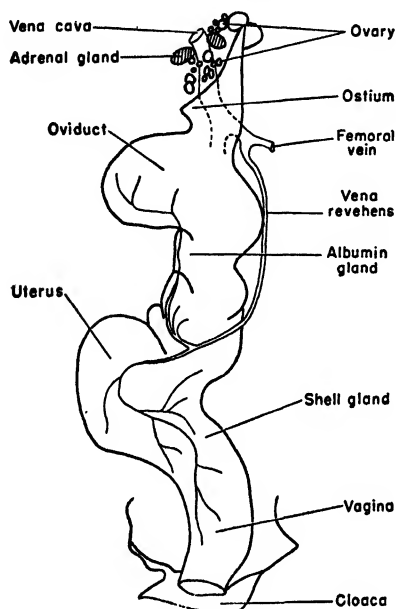


FIG. 220A. The female avian reproductive system. One müllerian duct is greatly developed and coiled in connection with albumen and shell secretion and with the transportation of the relatively large egg to the cloaca.

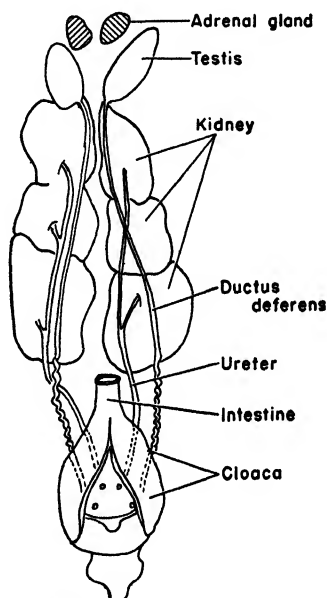


FIG. 220B. The male avian reproductive system. The gonads are greatly reduced in size except in the breeding season. External reproductive organs do not occur.

cloaca underneath the skin; one or the other of these sacs is everted and inserted into the cloaca of the female during copulation. A groove in its medial wall makes a passageway for the introduction of sperm. *Sphenodon*, the primitive lizard, is without copulatory organs, but internal fertilization is accomplished by cloacal approximation.

Birds. Female. The müllerian ducts originate as paired tubes in both male and female birds. In the male they disappear during embryonic development. In the female the left, duct retained in many species,

becomes the functional oviduct (Fig. 220A). The right ovary may disappear entirely or remain as a vestigial organ. The functional ovary lies dorsally in the abdominal cavity and in the resting stage is quite small. It is covered by the peritoneal lining of the body cavity. A mesovarium supports the organ dorsally. Adrenal glands are in close proximity, usually dorsally to it, as is also the inferior vena cava. The oviduct is characterized by a thin serosal layer, furnished by the peritoneal covering; a circular and a longitudinal smooth muscle layer, the tunica muscularis; and an inner, highly vascularized mucosa whose epithelial cells are ciliated. The glands that secrete egg albumen are in this mucosal layer. An ostium at the anterior end of the müllerian duct is in close proximity to the ovary. In the active state the tube is coiled in the common fowl. In the first coil nearest the ostium are the albumen-secreting cells; the second coil is narrowed and is known as the isthmus. Its tubular glands secrete a sticky colloidal substance which precipitates into threads and forms the thin, skin-like layer over the albumen. The third coil, the uterus, is thick-walled and is the site where the shell is secreted about the egg. Calciferous glands in the mucosal walls overshadow the remaining structures in this area. The circular muscular layer is augmented at both upper and lower ends of the uterine portion to form sphincter muscles. The final division, the muscular vagina, opens into the cloaca (urodeum) lateral to the left ureter. Mucus secreted by the glands in the vaginal division lubricates the egg surface during the act of laying.

Male. The male reproductive system includes testes, ducts, and copulatory organ (Fig. 220B). The testes lie in the body cavity at the cranial margin of the metanephros, lateral to the postcaval vein. Tubuli contorti constitute the functional tubules of the testis. They differ markedly from the mammalian tubules, in that they form an elaborate anastomosing network. Another peculiarity of these tubules is their periodic degeneration. During the sexually active period, 200 to 300 times as many tubules appear as during the inactive. Their volume is in the ratio $\frac{1}{27}:1$ in *Passer domesticus*. In the quiescent period the gland is barely discernible. Elements of the mesonephros furnish the vasa efferentia. The epididymis into which the vasa efferentia lead undergoes great variations in size, correlated with comparable changes in the testis. The vas deferens descends more or less parallel with the ureter and opens into the urodeum lateral to it. In the fowl and duck (*Passeres*, *Anseres*, *Columbae*, *Gallus*) a seminal vesicle occurs at the posterior end of the vas deferens. A penis is absent in most birds, and sperm is introduced into the female of such species by evagination of the proc-

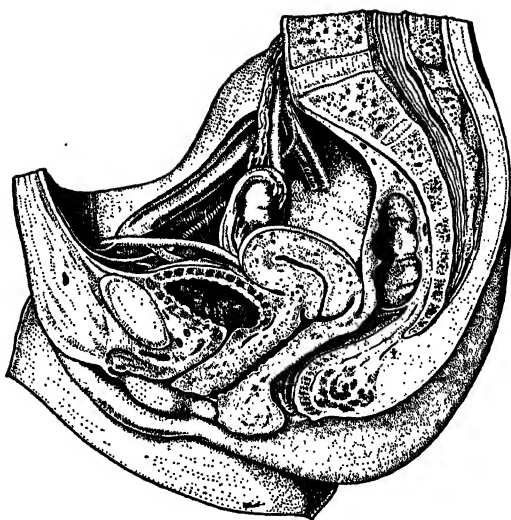
todeum of both male and female after their approximation in copulation. Sperm is then introduced into the urodeum.

In certain nonflying birds and aquatic fowls like the duck a penis is developed in the male and its homologue, a clitoris, in the female. Absence of a penis is believed to be a secondary condition.

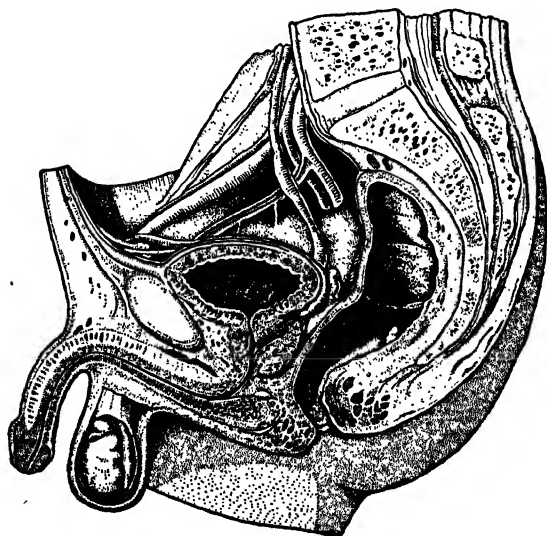
Mammals. It will be recalled that the mammals are subdivided into three great groups, Prototheria, Metatheria, and Eutheria. This division is based upon a number of characters peculiar to each group, and among these are certain features of the reproductive system. Thus, the ovary, which is a small, compact, ovoid organ in the levels above the monotremes, is reptilian or bird-like in the Prototheria, a condition associated with the large amounts of yolk present and with their egg-laying habits. A further characteristic in this group is the single left ovary. The oviducts, or müllerian ducts, open in the usual manner in the monotremes. An egg case, secreted by the thickened part of the duct known as the uterus, opens into a urogenital sinus and thence joins the cloaca.

In marsupials and in the Eutheria the ovary is small. It tends to be displaced caudally from its original site high in the pleuroperitoneal cavity. Müllerian ducts, or *oviducts*, terminate in the body cavity by *fimbriated ostia* in close proximity to the body of the ovary. In some rodents as well as in certain other groups a bursa at the ostial-ovarian junction apparently prevents loss of the egg in the abdominal cavity.

Fusion of the oviducts together with proliferation of smooth muscles forms the thick-walled *uterus* (Fig. 221A). The latter terminates in a canal, the *vagina*. This is formed by the fused portion of the müllerian ducts which originally marked the anterior end of the urogenital sinus. Not all uteri are single, and in the so-called *uterus duplex* the two divisions do not join above the level of the vagina. In the marsupials, rodents, and elephants, this division represents a still more primitive state in that the entire oviduct, the uterus and vagina, remains separate from its fellow, thus resulting in paired organs. In the carnivores and in some ungulates the posterior ends of the uteri are fused, forming the *bipartite type of uterus*; a further step is represented by the *bicornuate type*, in which only the cranial ends are not fused. This is characteristic of the perissodactyls (horse, ass, zebra), most of the cud chewers, and the insectivores. The single, completely fused *uterus simplex* finally marks the monkeys, apes, and man. The vagina opens externally into a *urogenital canal* of varying length; in the human female it forms the short *vestibulum vaginae*; in many other mammals it is more elongate and represents the common urinary and genital duct, the homologue of the urethra.



A



B

FIG. 221A and B. Sagittal section through human female and male generative organs. Note the separate urethral and vaginal openings in the female; the external testes (*B*) in comparison with the internal ovary; the thick-walled uterus.

The male testis, or generative organ, originally develops inside the body cavity (Figs. 221, 222). Later it has a varied history. In some mammals it is retained in the body cavity, *e.g.*, in the elephant, rhinoceros, and aquatic mammals; in others it descends into an extension of the abdominal cavity, the *scrotal sac*. In a few it may be retracted into the abdominal cavity even though it is normally in the scrotum proper. This is the situation in many rodents. Still another state is represented in a large number of mammals, including artio- and perisso-

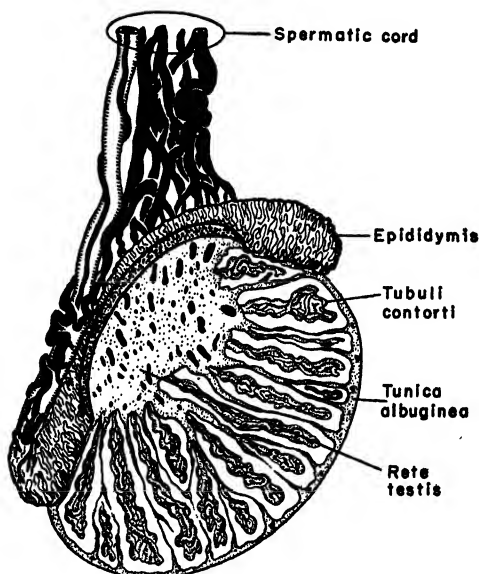


FIG. 222. Section through the mammalian testis. In addition to producing sperm in the tubules of the testes, interstitial cells surrounding the tubules secrete a male (androgenic) hormone.

dactyls and primates, in which the testis normally descends into the scrotal sac and remains there permanently.

The testis is ovoid in shape, correlated in size with that of the animal. In a male elephant of 14,670 lb., which the author dissected, these glands weighed 20 lb. The gland is covered by a heavy, white connective-tissue layer, the *tunica albuginea*, surrounding a thin serous extension of the peritoneum, the *tunica vaginalis*; in those forms in which the testis is retained within the body this last is simply the reflected peritoneal covering over the gland.

Essential internal features of the mammalian testis include the tubes in which spermatozoa are formed; these include the *tubuli contorti*, which extend peripherally to the *hilum* of the testis, where they become straight and are called the *tubuli recti*; these anastomose in turn into an elaborate network, the *rete testis*. These testicular derivatives meet the head of the *epididymis*, which represents the genital part of the mesonephros and hence is a mesonephric derivative. A number of these transformed mesonephric ductules join the rete testis. Known as *efferent ducts*, they enter the mesonephric duct proper. This has become greatly coiled and differentiated into the epididymis, which in turn becomes continuous with the *ductus deferens*.

To understand the further relations of the ductus deferens to the penis, the bladder, and the urethra, it is necessary to examine their embryology briefly. Originally the mesonephric ducts end in the cloaca, into which the intestine also opens. It will be recalled that the ureter, or urinary tube, grew craniad as a new development from the mesonephric ducts with the appearance of the metanephros, at the point where they join the bladder. These ureters eventually open directly into the cloaca in the embryonic state. In addition the stalk of the allantois also connects with the cloaca. A urorectal septum divides the cloaca into dorsal and ventral halves at this stage. Into the dorsal extends the rectal part of the intestine, while the ventral is further subdivided into a cranial portion, which differentiates into bladder and urethra, and a caudal part, the urogenital sinus. This last represents a caudal extension of the urethra. The ductus deferens of each side opens into it. Thus, the anatomical relations, as they appear in the adult, are established, namely: a bladder into whose base the paired ureters open; the neck of this bladder is continuous with the short *urethra*; this joins with the *urogenital canal* and extends to the terminus of the *penis*. This urogenital canal begins at the *ejaculatory ducts*, where the ducti deferentes open into it.

In the Prototheria, where the cloaca is retained, the urogenital sinus continues to open into it. The ducti deferentes enter it dorsally, while craniad a ventral evagination from its wall forms the bladder. The monotreme cloaca, according to Keibel, is an ectodermal invagination, added to the endodermal cloaca typical of reptiles and birds.

The *prostate gland*, which usually surrounds the junction of urethra and urogenital canal, is a derivative of the latter, just as are *Cowper's glands*. Both glands open into the urogenital canal. In the female, the homologue of Cowper's glands, *Bartholin's glands*, likewise enter the urogenital sinus. The smooth muscle capsules of these glands are supplied by the urethral covering, *i.e.*, the body of the prostate develops and extends under the smooth muscle coat of the urethra.

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CHAPTER 12

THE ENDOCRINE GLANDS

HISTORICAL

Inquiries into no other organ system have aroused the interest or curiosity that greeted the advances in the field of endocrinology in the past two decades. Knowledge of the profound effects exercised by certain body organs goes back to early Egyptian and Greek cultures. Not only did the ancients have academic knowledge of the effects of castration, for example, but they practiced this type of mutilation quite commonly. This does not imply that the physiology involved in the operation was known, except as it was expressed in changed behavior and loss of sexual functions. In like manner, Paracelsus (1493-1541) apparently was aware of some of the disturbances that occurred in the thyroid gland and by empirical means attempted to reduce goiter. Present interest stems in part from the dramatic effects reported after hormone injections, the spectacular publicity given to Steinach's monkey-gland experiments of the early twenties, the widespread advertising of hormones, as well as from the eternal quest for the Fountain of Youth, which everyone seeks but few find. The rejuvenating effects of hormones in common use today are well known and publicized, and our interests are easily awakened when these agents and their powerful generators, the ductless glands, are mentioned.

It was not until the middle of the past century (1849) that the functional relationship between testis and body was experimentally established in the fowl by A. Berthold. In a brief report, now a classic, of his experiments in removing and transplanting the testes in fowls, he expressed for the first time our modern conception of the *modus operandi* of internal secretion. In describing the results following transplantation of the testes, he stated that, so far as voice, sexual urge, belligerence, and growth of comb and wattles were concerned, the birds remained true cockerels, and since the original nerves were no longer connected to the testis, it followed that the testes acted through the blood stream and consequently upon the entire organism. In other words, this gland contributed some product to the blood which in turn affected one or more systems remote from its site. Essentially this is our modern conception of hormonal secretion and action.

The older ideas that executive control of the body resided in brain or heart stemmed no doubt from experiences in the hunt or from early critical experiments in which necks were severed, heads bashed in, or hearts cruelly but skillfully excised by high priests of religion or by soldiers in war. This viewpoint of the nervous system had to give way when the executive potency of ductless glands first became recognized. Today no one disputes the fact that for the maintenance of the body parts whether muscle, gland, or organ, nervous control is essential, but in addition no physiologist denies that a balanced endocrine system is also requisite.

GENERAL NATURE

The endocrine glands at first glance do not present the unified or integrated front exhibited by the various parts of the nervous system, although there is an underlying coordination and cofunction of the various glands comprising the system. Thus the several activities of the anterior lobe of the pituitary gland are interrelated and integrated with the functions of gonads, thyroid and adrenal glands, as will be shown when these glands are examined in greater detail.

The question of the origin of the entire endocrine complex offers problems. To begin with, the origins of the several glands must be considered separately, since, with the exception of the glands of branchial origin, each appears to arise independently with no connections to the others. Further, the glands have no exact or near counterparts in the invertebrate world, although a substance akin to adrenalin has been found in the leech by Elliot and Swale Vincent, and the pigment cytochrome appears necessary for rapid muscle contraction in insects. Other hormones, *e.g.*, a molting and a pupation hormone, have been disclosed in insects associated with the ring and prothoracic glands. Endocrine glands, however, appear to be independently developed, adaptive mechanisms in the vertebrates, by which various cyclical or regulatory activities of their highly complex bodies are maintained, and through which energy may be utilized in a more life-conserving fashion than is possible in unicellular or primitive metazoan organizations. Their effect on the nervous system will be dealt with in the description of the individual glands.

Control in the body is exercised through nervous stimulation (electrical) and through chemical (humoral) agents. Endocrine glands invariably utilize the chemical, *i.e.*, humoral, means of stimulating near or distant parts. Of late it has been discovered that the nervous system is not limited to electrical, or nervous, stimulation but also produces effective stimulation through humoral secretions. Thus sympathetic

nerve excitation releases a hormone, sympathin, at the nerve-smooth muscle junction, and vagal stimulation liberates acetylcholine secretion at the vagal-cardiac junctions. These humors engender a chemical effect, just as do the hormones released by the endocrine glands.

Cowdry has differentiated the endocrine glands on the basis of specialization. According to that author, the first stage in such specialization occurs when a tissue, in addition to a given function, acquires other functions whose effects are transmitted through the blood stream, *e.g.*, gastric mucosa and duodenum. The mucosa, in addition to its exocrine secretions into the lumen of the intestine, passes endocrine secretions directly into the blood stream. Another stage appears when glands of recognizable specialization, perhaps having an original exocrine function, bud off some cells with specific endocrine functions, *e.g.*, thyroid and parathyroid glands. A fourth is reached when two groups of cells appear in a common gland such as the cortex and medulla of the adrenal gland and the anterior and posterior lobes of the pituitary body. Such cells have unrelated endocrine functions, although they may be closely associated with each other.

The endocrine glands exhibit varying degrees of complexity with reference particularly to their immediate associations. Thus the thyroid gland cells are of one type, with highly specific metabolic functions, but associated with them are small parathyroid masses with equally specific but distinctive calcium regulatory tasks. In the male gonads we find a group of interstitial cells, apparently the only elements with an endocrine function in close association with sperm-forming cells; in the ovary, epithelial cells furnish the follicular liquid and estrin, and corpus luteum cells secrete the luteal hormone, or progesterin, in close proximity with the ova.

The following brief descriptions of the structure and functions of the glands can point out only a few significant facts. For detailed accounts the student is referred to the volumes devoted to this field.

PINEAL BODY

This is a small oval body emerging by a stalk from the roof of the diencephalon, over the third ventricle, and lying in the sulcus of the superior pair of the corpora quadrigemina (Fig. 223). It is an epithelial body within a connective-tissue covering. An estrogenic secretion has been postulated for the gland. This idea is based on implantation of pineal bits into castrated mice with resulting stimulation of the generative organs, comparable with that of estrogenic injections. Others believe it causes growth acceleration when the substance is fed to young

animals. Roundtree and his associates report that pineal extract causes a retardation of growth, or dwarfing, in successive generations of rats, associated with an accelerated sexual development. Abnormal sexual development, rapid growth, and precocious mental development have also been attributed to pineal tumors. Calcifications are frequent in the gland.

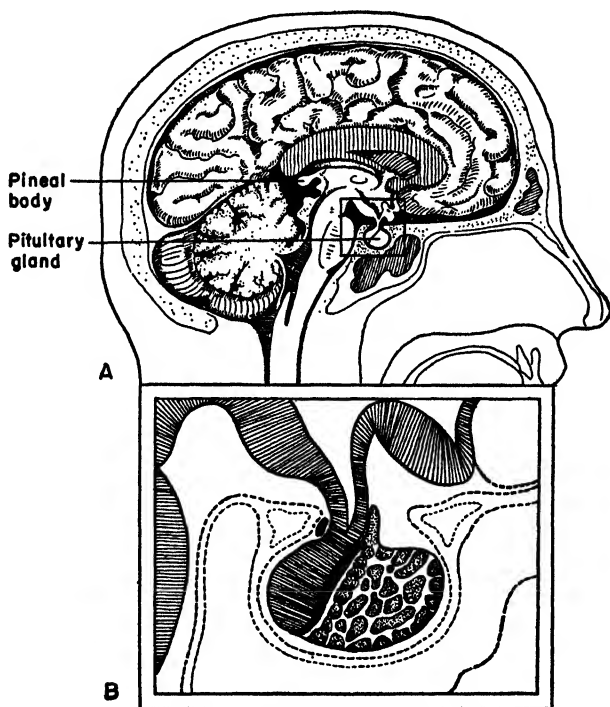


FIG. 223A. Pineal body and pituitary gland. The pineal body is connected with the roof of the diencephalon by a stalk. In reptiles it has the characteristics of a simple eye. B, detail of pituitary gland.

THE PINEAL EYE

In reptiles and tailed amphibians and in *Petromyzon*, the pineal body has the characteristics of a simple eye. The small subcutaneous vesicle is associated with the chorioid plexus of the diencephalon by a stalk and supplied by a pineal nerve. In reptiles, in addition, a parietal eye develops under cover of the pineal organ and lies in the hollowed-out for-

amen of the skull. A parietal nerve, which is sensory and homologous to the retina, passes from the base of the parietal vesicle to the habenular commissure of the brain. The area over the eye is free of pigment and presumably permits changes in light intensity to affect the parietal organ.

THE PITUITARY GLAND

The pituitary gland develops from two diverse and entirely separate parts: the *posterior lobe* originates from the floor of the diencephalon

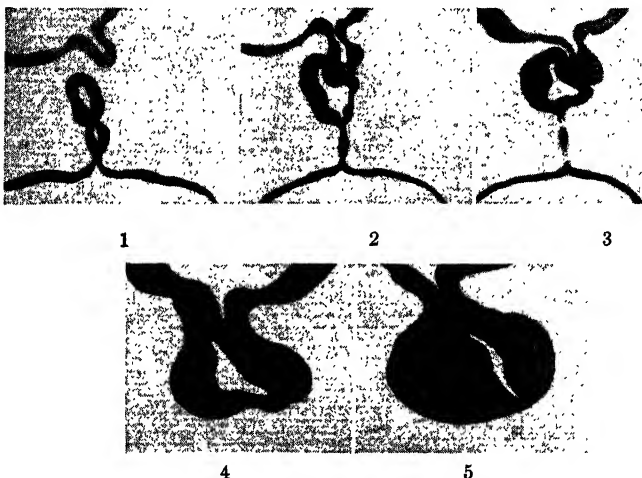


FIG. 224A. Development of the pituitary gland. 1, 2, 3, early stages showing approximation of Rathke's pouch from below and evagination of pars nervosa of pituitary gland from above. In 3, Rathke's pouch has almost lost its connection with the roof of the mouth. 4, 5, final stages in development, black portion represents the anterior lobe contributed by Rathke's pouch, gray portion, the posterior lobe contributed by the brain floor. (Courtesy of Armour Laboratories, Chicago.)

associated with the *infundibulum*, the funnel-like outpocketing of the third ventricle; the *anterior lobe* is an ectodermal derivative from *Rathke's pouch*, the latter an evagination in the roof of the embryonic mouth (Figs. 223, 224).

With continued embryonic development the epithelium of the anterior lobe loses its connection with the roof of the mouth and more or less completely surrounds the posterior lobe. Its upward extension, where it approaches the floor of the diencephalon, is the *pars tuberalis*, derived from the anterior lobe. The *pars intermedia*, also an anterior lobe

derivative, lies posterior to a cleft in the anterior substance, the remnant of the lumen of Rathke's pouch. The cleft separates a small portion of the anterior lobe tissue from the main body of the lobe and causes the

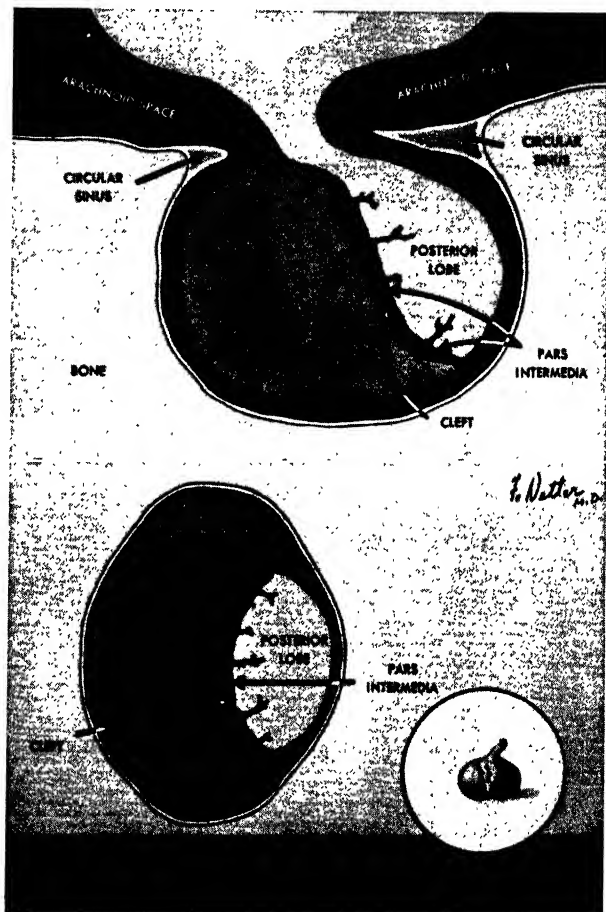


FIG. 224B. Detail of the interrelations of the various parts of the pituitary gland. (Courtesy of Armour Laboratories, Chicago.)

smaller part (pars intermedia) to be joined with the posterior lobe. The part of the anterior lobe anterior to the cleft is also known as the *pars distalis*. This is continued around the stalk as the *pars tuberalis*.

Posterior Lobe. The posterior lobe (*pars nervosa*) is an outgrowth of the third brain ventricle; more specifically, its cells originate from the ependymal layer. The structural elements are *pituicytes*, *neuroglial cells*, and *nerve fibers*. The pituicytes are branched cells, presumably responsible for the secretion of the posterior lobe.

The neuroglial cells apparently are the forerunners of the pituicytes, since their differentiation into the latter has been observed. Two nerve tracts, the *tuberohypophyseal* and the *supraopticohypophyseal*, connect the diencephalon with the posterior lobe. The anterior lobe has no such direct nerve connections; it is supplied however by *sympathetic fibers* that ascend along the carotid arteries as the carotid plexus.

The posterior lobe through its extract acts in at least three specific ways: (1) it produces an antidiuretic effect (diabetes insipidus appears after degenerative lesions of the posterior lobe); (2) it causes selective contraction of smooth musculature of the cardiovascular tree, the intestinal, renal, and respiratory systems; and (3) it acts selectively on the uterine wall by stimulating uterine contraction.

An active principle, *pitressin*, from the posterior lobe, responsible for the generalized effect on smooth muscle, is frequently employed pre- and postoperatively in maintaining or restoring smooth muscle tonus of the tract.

Pitocin, the active principle affecting uterine musculature, also a product of the posterior lobe, is frequently used to check uterine bleeding in labor and in the restoration of the uterus to its normal size. Secretion of the antidiuretic hormone depends on the integrity of the nerve connections, for when these are severed, diabetes insipidus results.

Pars Intermedia. The *pars intermedia*, which it will be recalled is also an epithelial derivative of Rathke's pouch, contains a quantity of hyaline colloidal material. Its cells are *chromophobic*, which means that they resist staining. These cells are similar to the chromophobe cells of the anterior lobe. A second type of cell, the *basophilic cell*, is sometimes found. The only function definitely verified for the *pars intermedia* is its effect on pigmentation. Experiments have shown that the pigment cells of some cold-blooded animals may be expanded by the active substance called *intermedin* by Zondek and Krohn, who first isolated it.

The Anterior Lobe. The anterior lobe is characterized by three types of cell (Fig. 225), which appear in about the following proportions in the human gland: (1) chromophobes, 52 per cent; (2) acidophils, 37 per cent; (3) basophils, 11 per cent. These percentages change after castration, in pregnancy, with the estrus cycle, or following removal of other endocrine glands. Apparently these three cell groups are derived from a

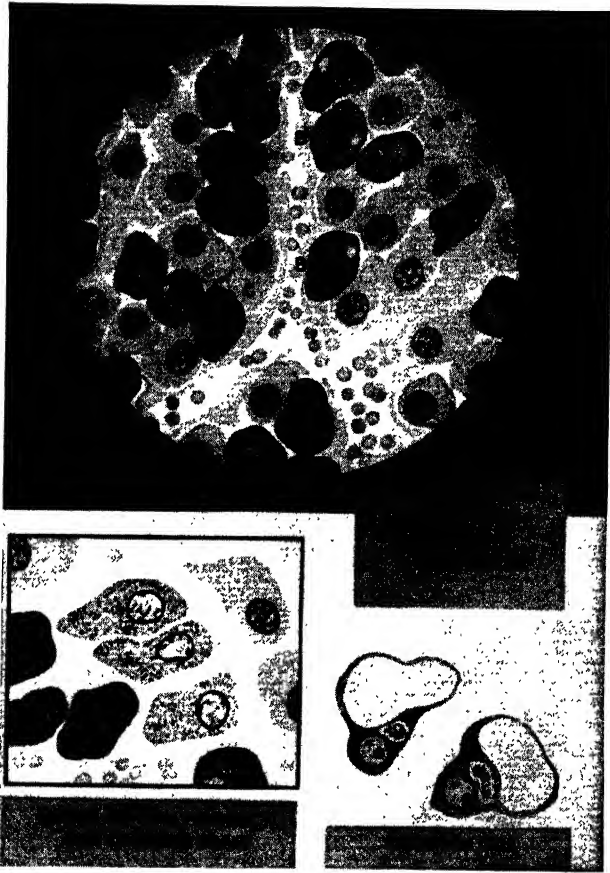


FIG. 225. Types of pituitary cells. (Courtesy Armour Laboratories, Chicago.)

single type, the chromophobes or their forerunner; only the acidophilic and basophilic cells are known to be secretory.

A variable number of functions have been assigned to the extracts of the anterior lobe. Specifically verified are the following effects, which depend upon one or more active principles elaborated by the anterior lobe:

- | | |
|------------------------|-----------------|
| 1. Growth-somatotropic | 4. Gonadotropic |
| 2. Thyrotropic | 5. Lactogenic |
| 3. Adrenocorticotropic | |

Other effects which have some experimental support to verify the existence of a definite principle or principles are the following: diabetogenic; pancreatropic; metabolic; parathyrotropic; hematopoietic.

Because of these manifold influences upon the body or upon specific organs, the pituitary gland may properly be called the master gland of the body. No other gland, save the liver, approaches it in variety and

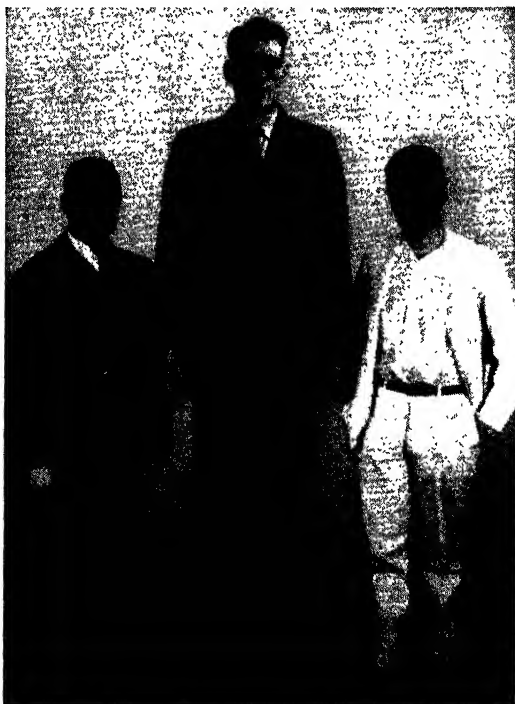


FIG. 226. Overgrowth caused by excessive secretion of "growth principle" of the pituitary gland.

complexity of functions. The brief summary of its activities included here applies most widely to the mammals, in which the gland has been studied extensively.

Growth Principle. Experimentally it has been shown that overgrowth and gigantism may be produced in animals treated with extracts of the growth hormone (Fig. 226). This substance is secreted by the acidophilic cells. Hyperfunction of the anterior lobe may produce two types

of overgrowth. One of these, pituitary gigantism, results from overactivity of the eosinophilic (acidophilic) cells before the epiphyses have closed. It will be remembered that continued skeletal growth takes place at the cartilaginous junctions, or epiphyses, situated between the shafts and the heads of bones and in the skull sutures. After epiphyseal closure, normal skeletal increase in length no longer takes place. Overactivity of the growth hormone permits growth to continue indefinitely, through delay of suture closure. Certain types of neoplastic tumors of the anterior lobe result in more cells and more secretion and account for such gigantism. This may result in a stature of 90 to 93 in. or more in the human being.

A second type of overgrowth appears if the anterior lobe becomes overactive after suture closure. This results occasionally in the condition known as acromegaly. Literally this means gigantism of points. Such abnormality becomes evident in the cheekbones, the chin, the supra-orbital ridges. The hands and feet become spade-like, the ears overdeveloped, the tongue thick, the viscera enlarged along with the skeleton and musculature; the general effect is a grotesque caricaturization of the normal individual, both internally and externally.

Thyrotropic Principle. The relationship between thyroid and pituitary glands has been established through the effect produced on the hypophysis by thyroidectomy and, conversely, the effect on the thyroid by hypophysectomy (Fig. 227). A thyroid-stimulating agent occurs in the hypophysis; its suppression leads to reduction in thyroid activity as well as thyroid size. Hypophysectomy of the tadpole causes a failure of metamorphosis, presumably through inactivation of the thyroid gland. Addition of thyroid extract in such a hypophysectomized animal induces metamorphosis.

Adrenocorticotropic Principle. Just as the interrelationship of thyroid and pituitary gland was determined by removal of one or the other gland, so adrenocorticotrophic relations have been established (Fig. 228). Hypophysectomy causes degenerative changes in the adrenal cortex which may be restored by pituitary implantation. Overactivity of the anterior lobe associated with increase in the basophilic cells has been associated with overdevelopment of the adrenal cortex. Recently it has been discovered that this hormone has powerful effects in eliminating arthritic pain. Apparently it causes the adrenal cortex to liberate a hormone, cortisone, which acts specifically in arthritis.

Gonadotropic Principle. The story of the discovery of the interrelationships between pituitary gland, testis, and ovary has more unexpected and unpredictable angles than a mystery novel (Figs. 229, 230). It has

been established with certainty that the anterior lobe of the hypophysis secretes a stimulating hormone which causes the ovarian follicle to develop, ripen, and discharge; that it produces another hormone which induces the growth of a corpus luteum at the site of the ruptured ovarian follicle. The follicle-stimulating hormone is commonly designated as F.S.H.; the luteinizing hormone as L.H. Comparable action, particularly by the L.H., on the testicular interstitial cells of the male not only

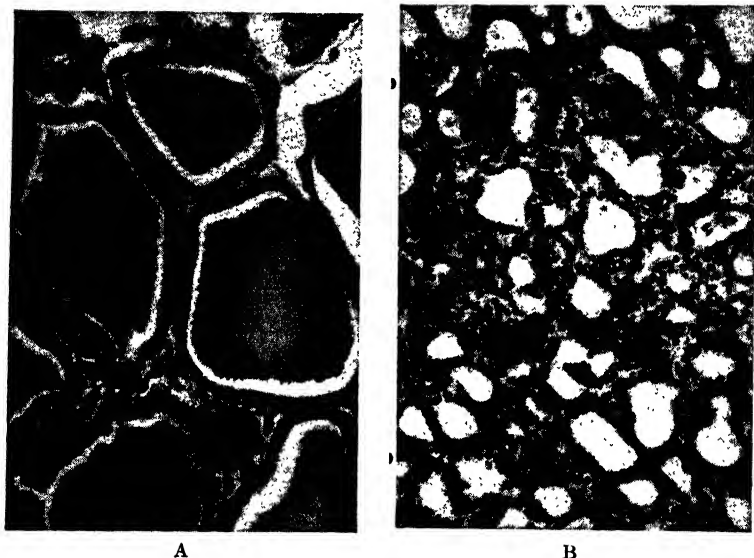


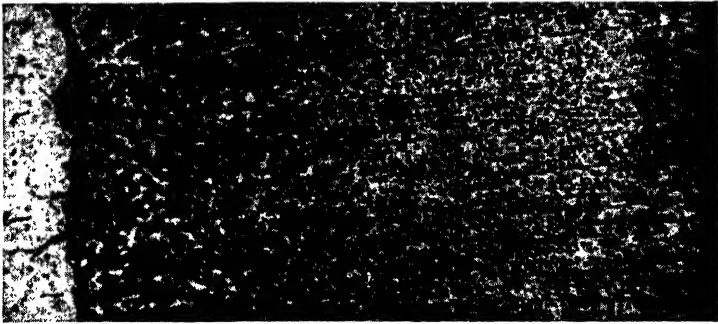
FIG. 227. Effect of thyrotropic hormone injection. *A*, thyroid gland (rabbit) in quiescent state, cells, low cuboidal in type, colloidal secretion copious; *B*, thyroid gland (rabbit) in highly active state, hyperplasia represented by great increase in number of cells, and decrease of colloidal secretion.

controls their development but secondarily determines the male characteristics.

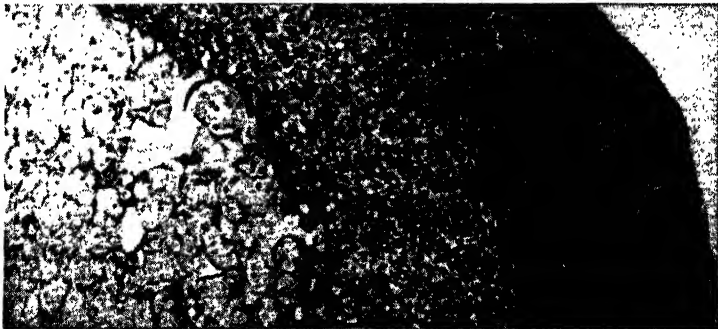
It is known today that during pregnancy the chorion, the embryonic contribution to the placenta, secretes gonadotropins, with some effects akin to those of F.S.H. and L.H. Although the chorionic gonadotropins apparently are unable to ripen the ovarian follicles in the female, they stimulate the interstitial cells in the male. Another source for gonadotropins is pregnant mare's urine. Gonadotropins from this source induce follicular and corpus luteum development. The effects of follicular and

corpus luteum secretions will be described in the account of the testis and ovary as endocrine glands.

Lactogenic Principle. This extract is known to induce milk secretion in virgin mammals as well as in male mammals (Fig. 231). It induces



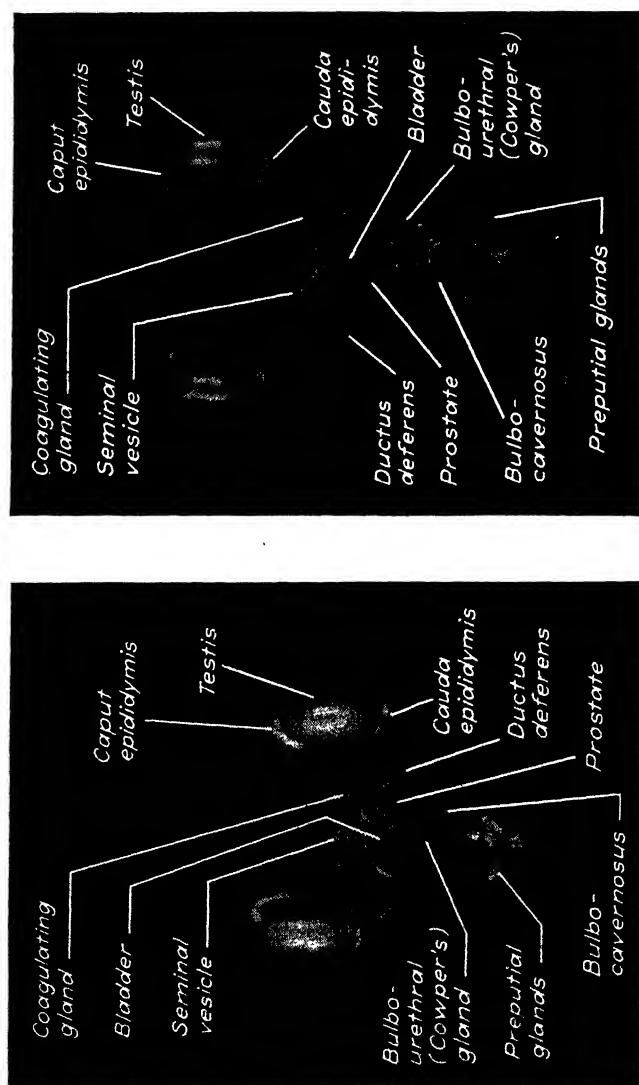
A



B

FIG. 228. Effect of hypophysectomy on the adrenal cortex of the rat. *A*, normal adrenal cortex, extending from medulla on left to capsule on right. The three cortical areas; glomerulosa, fasciculatis, and reticularis are defined. *B*, effect of hypophysectomy. By loss of cytoplasm from individual cells in all three zones, the cortex has become atrophic. Medulla is unchanged. Total weight of gland one-third normal. (Courtesy Parke Davis and Co., Detroit.)

crop enlargement and secretion of "pigeon's milk" in pigeons and the "setting" instinct in common fowls. Oscar Riddle and his coworkers isolated the effective substance, which they called prolactin. Production of milk secretion in male mammals after injection of the hormone is evidence for the potency of the lactogenic hormone.



(Courtesy of Dr. Warren O. Nelson, and Parke Davis and Co., Detroit.)

B

A

FIG. 223.

Evidence is accumulating that the anterior hypophysis secretes a diabetogenic agent that sensitizes the body to insulin. Depancreatized animals, for example, have been kept alive without insulin for several months following hypophysectomy, while with a normal hypophysis they pass quickly into diabetes and death after pancreas removal.

It appears likely that in time other specific pituitary principles or hormones may be uncovered. It is possible that new relationships may be disclosed with other systems that do not require the postulation of additional or new secretions. It is probable also that the verified effects described above are due to a highly complex molecule or molecules, as was suggested by Collip in 1937, rather than to a series of distinct hormonal secretions.

Whatever the exact mechanism of the pituitary gland may be, the relationships are sufficiently widespread to warrant its designation as master gland.

THE THYROID GLAND

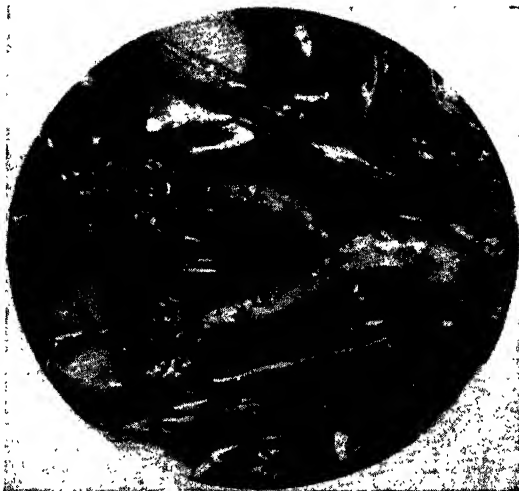
While fanciful anatomical descriptions of the pituitary gland go back to Galen (110 A.D.), accurate knowledge of the thyroid gland dates to the last century and precedes valid findings about the pituitary. Until two or three decades ago the pituitary gland was frequently looked upon as a vestigial organ with no specific or vital function. On the other hand, from the middle of the last century, pathological conditions had been recognized and described in the thyroid gland. As a matter of fact, it is

FIG. 229. These photographs show the effect of Antuitrin S (injected twice daily for eight days) on the genital system of the immature white rat. Injections were started at 30 days of age. Dissected genitalia of a litter-mate control are shown on the left, those of the treated animal on the right. Note the markedly increased size of the seminal vesicles and of the bulbo-urethral glands in the treated animal. Testicular size in the treated rat was almost the same as that of the control, but histological sections of the treated organs reveal that interstitial tissue is considerably increased in amount.

	CONTROL	TREATED
Body weight	117.00 gm.	115.00 gm.
Testis	1.37 gm.	1.44 gm.
Seminal vesicles	5 mg.	51 mg.
Seminal vesicles (without secretion)	5 mg.	21 mg.
Prostate	7 mg.	20 mg.



A



B

FIG. 230. The effect of the anterior pituitary lobe hormone upon the female generative system of the rat. *A*, ovaries and uterus of untreated immature rat (approximately $\times 10$). Used as control in standardization of anterior pituitary and anterior-pituitary-like (Antuitrin S) gonadotropic extracts. *B*, ovaries and uterus of immature rat (approximately $\times 10$) after treatment with gonadotropic hormone from pregnancy urine (Antuitrin S). This reaction forms the basis of standardization of Antuitrin S.

stated that the great Paracelsus was able to reduce goiters with his famous Siebenbürger salts, one of whose elements was iodine obtained from the ashes of seaweed.



FIG. 231. The effect of the lactogenic hormone of the anterior lobe of the pituitary gland upon the mammary glands of the rabbit. *A*, in the normal adult female rabbit the mammary gland consists of only a limited duct system with a few secretory alveoli. Although not generally used to standardize lactogenic hormone, the rabbit is often useful in demonstrating its action. *B*, after two weeks of pseudo-pregnancy, induced by Antuitrin-S treatment, this animal has received pituitary lactogenic hormone. Milk secretion has occurred in the terminal buds and milk has begun to accumulate in the ducts. Lactogenic hormone completes the development of the mammary gland. (*Courtesy of Parke Davis and Co., Detroit.*)

The thyroid gland arises as a median epithelial diverticulum of the pharyngeal floor and possibly from a pair of epithelial outgrowths of the fourth pair of pharyngeal pouches, in the mammalian series (Fig. 232). In *Amphioxus* and in the urochords it is foreshadowed by the endostyle, also an epithelial diverticulum, but ciliated and retaining its

connection with the pharynx. Presumably it does not elaborate thyroxin in the protochordates. In cyclostomes the original connection with the pharynx is lost after metamorphosis, and the gland takes on the vesicular character it reveals in the vertebrate thyroid body. It has been found that radioactive iodine may be stored in the endostyle of the ammocoetes larva, perhaps the best evidence of the kinship of the endostyle of cyclostomes with the thyroid gland of vertebrates. In the fish

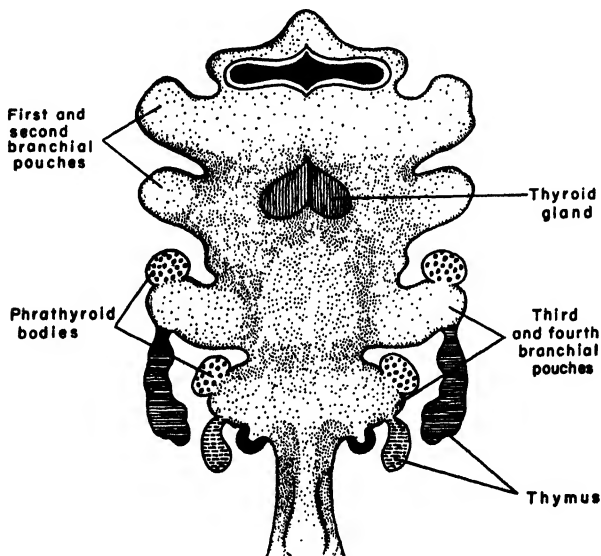


FIG. 232. Development of thyroid, parathyroid, and thymus glands. The thyroid gland develops from the floor of the pharynx; the parathyroids, usually four in number in man, develop from the lining of the third and fourth pair of branchial pouches; the thymus also develops from the third and fourth pair of branchial pouches.

the gland loses its pharyngeal connections embryonically, and the secreting epithelial tissue is segregated in a more or less compact mass, just anterior to the terminal bifurcation of the ventral aorta. It is not characterized by a high vascularity in the fish. In amphibians the gland is quite superficial under the loose skin underlying the lower jaws. Right and left glands are divided and are in close approximation to the carotid arteries. The gland has not been demonstrated in the aquatic cave-dwelling amphibian *Typhlomolge rathbuni*. In reptiles the thyroid body

is in the trunk cavity ventral to the trachea and some distance below the larynx. In crocodiles it forms an egg-sized mass rostral to the heart with some evidence of division; in alligators it is completely divided into two lobes. In turtles and snakes the single thyroid gland appears more vascular than in the Crocodilia. In birds it lies near the carotid-subclavian junction within the thoracic cavity, in quite close proximity to the heart, and definitely separated from the parathyroid glands. In mammals it is usually associated with the thyroid cartilage, although in a dissection on an African hippopotamus in the field the author found the gland at some distance from the head of the trachea, and partly intrathoracic.

The histological structure of the thyroid body is quite uniform throughout the vertebrates. The most striking feature in a stained section of the normal gland from almost any vertebrate specimen is the homogeneous colloidal material which is retained in many of the follicles.

The epithelial secreting cells are arranged in irregular follicles separated by connective tissue in which the blood and lymph vessels and the nerves are carried. In the normal state the cells lining the follicles occur as a low cuboidal epithelium. The lumen of the follicle is filled ordinarily with the homogeneous colloidal substance. The epithelium exhibits a peculiarity in that a basement membrane is lacking. This is of significance during secretion and during absorption of the substance secreted in the follicle. The epithelial cells vary in size and number, depending upon the activity of the gland. In the hyperactive state a hyperplasia, or abnormal increase, of epithelial cells may occur. The cells contain colloidal droplets, clear vacuoles and small granules, spherical nuclei and tiny nucleoli.

Vascular, lymphatic, and nerve supply to the thyroid gland is copious. In spite of the many studies devoted to it, little is known as to the mechanism of its secretion. Seasonal variations in secretion, evident responses to changed external conditions, occur. Iodine content of food and of water determines its size and degree of activity within certain limits. Under conditions of stress, conflict, and worry, so-called exophthalmic goiter may appear in man as well as in animals. In such cases the activity of the gland is enormously increased, and since its primary activity is to govern metabolism, this may be stepped up from 3000 to 10,000 cal. in a day in an individual with a normal output of 1500 cal. The active agent released by the gland is thyroxin, which is about 65 per cent iodine. The iodine content of dried thyroid tissue varies greatly. When it falls to 0.1 per cent or less, it implies an abnormality; the normal range is about 0.25 to 1 per cent of the dried gland weight. Just what

the role of thyroxin in the tissues is not known, but from its effects it is assumed that it acts as a catalyzing agent in speeding oxidation, although thyroxin disappears during this activity.

Besides governing the oxidation rate of the body, the gland exercises a profound effect on the central nervous system. The degree of nervous activity and the mental life of the individual, or rather the direction of his thought life, are closely linked to the degree of activity of the gland. Hyperactivity is accompanied by extreme nervousness, oversensitivity, frequent emotional crises; while hypoactivity brings, in addition to a decreased metabolism, a depressing effect on the mental life in which morbid thoughts, self-depreciation, and self-condemnation are visible expressions of the condition.

The secretion thyroxin increases the bioelectrical potential of various tissues in the body. Nerve, muscle, and glands, all respond to its effects, presumably through increased oxidation.

It has already been pointed out that the anterior lobe of the pituitary gland liberates a thyrotropic factor that activates the thyroid gland. A defective pituitary gland lacking the thyroid-activating principle might possibly account for the pathological condition known as myxedema. The two most common ailments are simple goiter, a compensatory enlargement correlated with iodine lack in food and water, and exophthalmic goiter, a toxic hyperactivity affecting the metabolism, heart rate, and nervous system, and producing the characteristic bulging of the eyes from which the disease derives its name.

Two other less frequent pathological states leave profound effects on their victims. These are cretinism, a defective development of the thyroid gland starting in fetal life; it may involve absence or embryonic destruction of the thyroid gland, and it affects both bodily and mental development permanently; the other malady, myxedema, marked by an insufficient secretion or an absence of secretion, starts later in life and is characterized by dropsy-like swellings, loss of hair, and dulling of the mind. Other infections, inflammations, or malignant growths also occur in the gland.

The arterial circulation of the thyroid gland is transmitted through an inferior thyroid branch of the subclavian and a direct branch or branches of the carotid artery. These arteries form numerous anastomoses, and ligation of one or the other does not seriously hinder the blood flow. Venous drainage, plexiform in nature, pours into the jugular and innominate channels. The nerve supply is by sympathetic branches from the cervical sympathetic ganglia.

Wild animals show few thyroid abnormalities unless they live in so-called goiter belts, when goitrous enlargements may appear. These

have been recorded in fish, birds, and mammals. When certain species are confined, *e.g.*, the African lion, the American raccoon, thyroid disturbances are frequent, in spite of adequate diets and competent care.

THE PARATHYROID GLANDS

Embedded in the thyroid glands in some animals (man, horse), more distantly associated in others (fowls, rodents), are the parathyroid glands (Figs. 232, 233). These are derived embryonically from the craniodorsal aspects of the third and fourth pairs of branchial pouches. In their

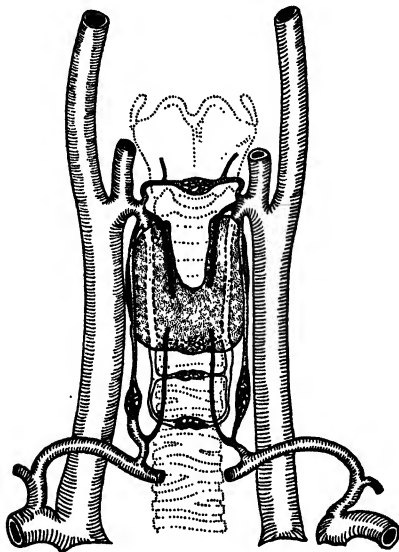


FIG. 233. Adult thyroid gland. The thyroid gland in the normal adult human being is shield-shaped and weighs about 25 gm. An isthmus joins the two lateral lobes. The gland is supplied by superior and inferior thyroid arteries.

development two types of cells, the *principal* with large nuclei and clear cytoplasm, and the *oxyphil*, larger and with a granular cytoplasm and relatively small nucleus, are formed. The glands are encapsulated.

Early knowledge of the functions of the parathyroid glands was gained largely from surgery on the thyroids. In the pioneering days of thyroid surgery it was found that tetany resulted from total removal of thyroids and parathyroids, while if the parathyroids were not removed, such a fatal result might not follow.

In 1909, MacCallum and Voegtlin observed that blood calcium was

greatly reduced after removal of the parathyroids in dogs. It was noted also that tetany could be relieved by administration of calcium or sodium salts. Today an extract which relieves tetany, and known as *parathormone*, is prepared from the parathyroid glands. It is known that the glands regulate calcium metabolism. Tetany, which is an intermittent spasmodic contraction of the muscles brought about by hyperirritability of the nervous system, appears when the parathyroids are underactive or inactivated, *i.e.*, when the blood calcium is low. Hyperactivity of the parathyroids, on the other hand, may result in hypercalcemia (excessive blood calcium) and in decalcification of skeletal substance. Apparently the osteoblasts (bone-building cells) and the osteoclasts (bone-destroying cells) are thrown into an imbalanced state by the hyperactivity of the glands, resulting in excessive osteoclast activity. The parathyroids are vitally necessary to the animal and to man. These glands do not occur in fish but appear in all other vertebrates above this level.

Parathyroids and Skeletal Formation. The daily calcium requirements in man are approximately 0.6 to 0.8 gm. During active growth much more is required. In like manner, pregnancy and lactation make heavy demands on the calcium of the mother. This calcium is utilized in skeletal growth. When the demands on the blood calcium drain the blood of its calcium, the deficit is made up from the skeleton, for the skeleton serves as reservoir for calcium and phosphates. Calcium salts are necessary for irritability of nerve tissue and muscle, for the permeability of cell membranes, and most obviously for skeletal growth. Absence of the proper proportions of calcium and phosphates in the diet leads to rickets in the growing child or animal. For the proper utilization of these elements, vitamin D, as well as the hormone secreted by the parathyroid bodies, is essential.

THYMUS GLAND

The thymus gland is an epithelial derivative from the third and frequently also from the fourth pair of branchial pouches (Fig. 232). The cell masses migrate caudally and dispose themselves on the pericardial sac, underneath the sternum. The tissue is present in all vertebrate classes. In the prepuberal stages in man the gland is pink in color and lobulated. Later it becomes infiltrated with fat. In the human being the weight at birth is 12 to 16 gm. This increases to 30 to 35 gm. at puberty. The young of all mammals exhibit sizable masses of thymic tissue, which disappears largely with sexual maturity.

Histological examination reveals numerous lobules separated by connective tissue; the lobules are composed of several follicles arranged into

cortical and medullary portions. The cortex is lymphoid, *i.e.*, it consists of lymphocytes and reticular cells arranged in a network. The medulla is made up of concentric layers of granular epithelial cells, the corpuscles of Hassall. The entire structure bears some resemblance to a lymphoid organ, rather than an endocrine gland. Blood supply is furnished by branches of the subclavian and internal mammary arteries. The innervation is both sympathetic and parasympathetic.

Loss of the gland apparently produces no noticeable effects on the experimental animal. Arrested gonadal development or castration retards its involution. In exophthalmic goiter it becomes enlarged, as it does also after adrenalectomy and hypophysectomy.

Precocious development of the animal has been brought about by injecting successive generations of white rats with an extract prepared from the thymus of young calves. This precocity included speeding the time of eye opening, tooth eruption, appearance of hair, ear opening, descent of testes, and opening of the vagina. This finding has not been generally verified. An indication of the dubious status of the thymus as an endocrine gland is offered by the following title of a recent exhibit by F. Gudernatsch: "The Thymus Is (Is not) an Endocrine Organ." In this exhibit the reasons he advances for considering the gland an endocrine organ are about equally balanced by those he offers against its endocrine functions.

GASTROINTESTINAL PRINCIPLES

Secretin is the name given to an agent released by the intestinal mucosa. It was discovered by Bayliss and Starling (1902) in the duodenum; they also gave it its name (Fig. 234). It is absorbed by the blood stream when the acid chyme enters the duodenum. The absorbed secretin causes the pancreas to secrete when the blood conveys it to that organ. The term *hormone*, which incidentally means to excite, was first used by the above-named workers to designate secretions that act through the blood stream and affect organs at a remote distance from the site of the secretion. Subsequently it has been found that the pyloric mucosal lining produces an extract which stimulates gastric secretion when injected into the blood stream. This extract has been termed *gastrin*. An agent having an inhibitory effect on gastric secretion and on the liberation of secretin has also been discovered in the mucosal lining of the duodenum and the pylorus. In the presence of neutral fats, this inhibitory agent, known as *enterogastrone*, is liberated by the duodenal mucosa into the blood stream and checks gastric secretion.

Other intestinal extracts have been prepared that presumably act

through the blood stream. Among these are *incretin*, prepared from the duodenal mucosa, which causes insulin secretion from the pancreas; *enterocrinin*, prepared from intestinal mucosa, which stimulates the intestinal glands to secrete the digestive ferment succus entericus; *chole-*

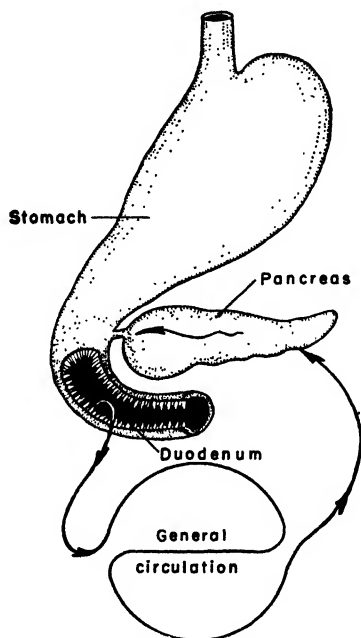


FIG. 234. Relation of secretin to pancreatic secretion. Secretin is liberated by the duodenal mucosa and absorbed by the blood stream. When it reaches the pancreas, it stimulates enzyme activity in that organ. These enzymes then pass into the duodenum.

cystokinin, elaborated in the duodenal mucosa in the presence of dilute and fatty acids, which causes the gall bladder to contract.

THE ISLANDS OF LANGERHANS

It has been known for over fifty years that complete removal of the pancreas caused sugar diabetes. The pancreas, functionally and structurally, is a dual organ with two types of cells (Fig. 235). One group secretes through ducts directly into the duodenum; the other, collectively the *islands of Langerhans*, consisting of isolated cell clusters, passes its

product, insulin, into the blood stream. The cells secreting through the duct produce digestive enzymes acting on the proteins, carbohydrates, and fats, while the islet cells control sugar metabolism. The islet cells differ among themselves, *i.e.*, two types, the *alpha* and *beta* cells, are recognized. To what extent the alpha cells contribute to the secretion is unknown. They are fewer in number than the beta cells. Activity of the islands depends on the sugar content of the blood. A hyperglycemia apparently causes them to secrete *insulin*, as the agent was called by Schäfer in 1916, with a resulting oxidation of the blood sugar, the building up of glycogen in the muscle and liver, and a retardation of the breakdown of liver glycogen. Whether or not the activity of the cells is dependent upon nervous action is not known.

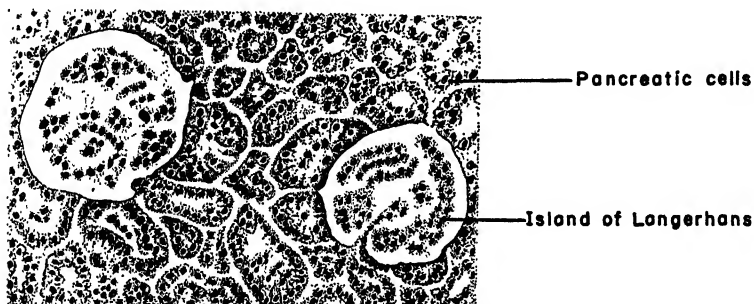


FIG. 235. The islands of Langerhans. These islands form small patches in the pancreas but do not pour their secretion, insulin, into the pancreatic duct. The secretion is taken up by the blood stream; it regulates sugar metabolism.

Failure of the islands to produce insulin results in sugar diabetes (diabetes mellitus). Adrenalin causes an increase in the blood sugar, counteracting the action of insulin, and capable of producing a hyperglycemia and glycosuria. An opposite effect, hypoglycemia, results when for any reason the secretion of the islands of Langerhans becomes excessive. This condition results in muscular weakness, disorientation and muscular incoordination, and convulsions. F. G. Banting, aided by C. H. Best (1921), was the first to demonstrate successfully the action of insulin by ligating the pancreatic duct in dogs and causing the acinus cells of the pancreas to degenerate without affecting the islands of Langerhans. An extract prepared from such material was effective in reducing the blood sugar and the glycosuria in diabetic animals. Subsequently it has been possible to obtain insulin from cattle and other animals. The islet cells occur in fishes as well as in all higher vertebrates.

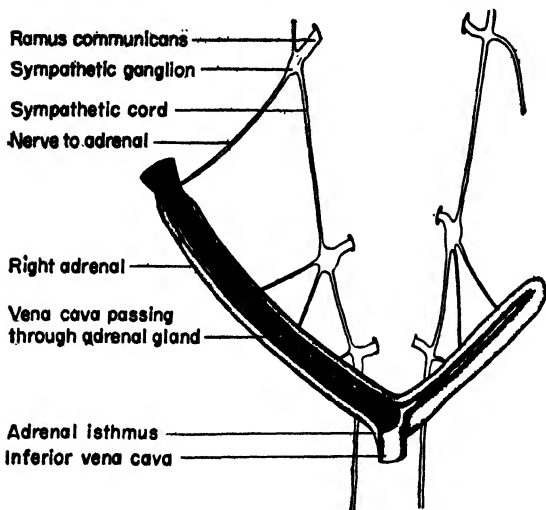


FIG. 236A. The adrenal gland of the alligator, showing close association with inferior vena cava.

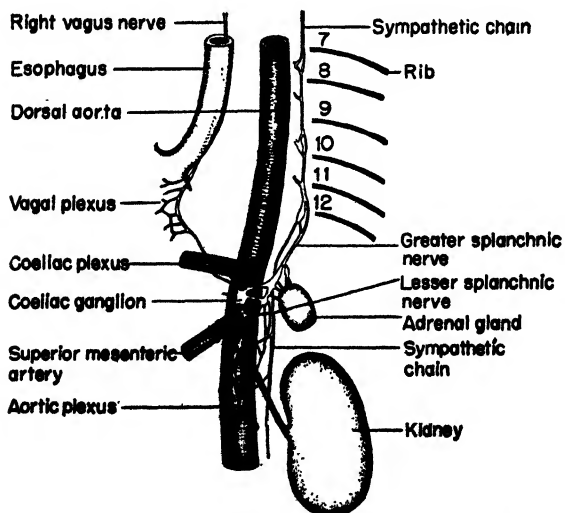


FIG. 236B. The adrenal gland of the rodent is usually located near the kidney; in the rat it is a small, rounded body.

THE ADRENAL (SUPRARENAL) GLANDS

The adrenal glands receive their name from their close proximity to the renal organs, or kidneys (Figs. 236, 237). This proximity does not occur invariably, however. In an 11-ft. manatee taken recently in Biscayne Bay, Florida, the author found the gland high in the thorax 34 in. distant from the kidneys; in amphibians, reptiles, and birds it is in close proximity to the gonads. The glands occur in all vertebrate groups, although in fishes the homologue of the cortex is buried in the

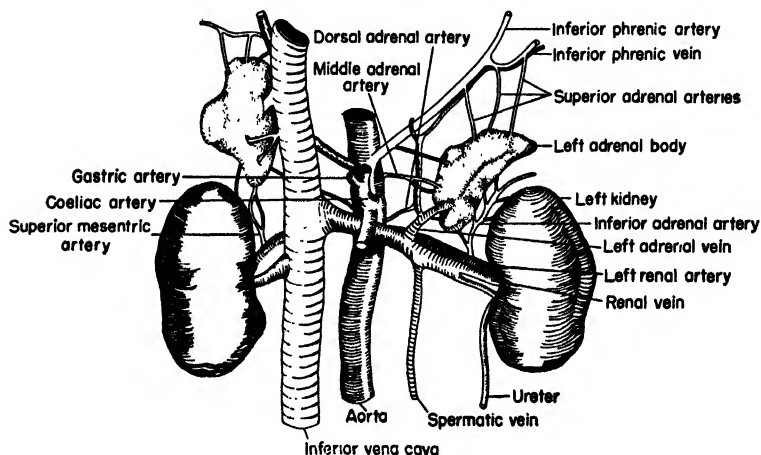


FIG. 237. In man, the adrenal gland is highly vascularized and has a large number of nerve fibers leading into it from the adrenal and celiac plexuses.

kidneys as interrenal tissue, while the homologue of the medulla appears as small, scattered clusters of chromaffin cells associated with the segmental sympathetic nerve fibers as they emerge from the spinal cord. The cells of the adrenal bodies are of dual origin. Those comprising the cortex are derivatives of the celomic epithelium; those of the medulla arise from cells similar to the forerunners of the sympathetic ganglia.

As stated, these two groups of cells are not found associated in the fishes. In *Amphibia* the chromaffin cells (the term is applied to cells showing a special affinity for stains) are intermingled with the cells of epithelial origin, and a clear distinction between cortex and medulla has not yet emerged. In reptiles and birds a closely similar pattern is fol-

lowed. In these two classes, however, larger aggregates of chromaffin cells cluster around the veins and sinuses within the glands.

In mammals a well-marked separation appears between cortex and medulla (Fig. 228). In his own studies the author has observed a capsule of connective and smooth muscle tissue surrounding the medulla in some of the large carnivores and ungulates and another capsule surrounding the gland as a whole. It should be recalled that the medulla constitutes the inner part of the gland.

Adrenal bodies are highly vascularized and highly innervated (Figs. 236A and B, 237). The chief arterial supply may arise directly from the aorta or from branches of the inferior phrenic artery. Venous drainage is largely from a central vein which traverses the medulla and sends many small twigs into its substance. Smaller veins drain the outer capsule and pass into the superficial vessels of the renal fat covering the kidneys. The central vein opens into the renal vein. The nerve supply emanates largely from the celiac plexus and the splanchnic nerves. The author has counted over 40 small nerve twigs passing into each human suprarenal gland, over 90 twigs entering the medulla of the tiger and the lion, and only 3 sympathetic twigs forming a small plexus entering the suprarenal gland of the alligator. Stimulation of the proper nerves increases the amount of adrenalin in the blood. The functions of the cortex and medulla are distinct and apparently unrelated. The cortex secretes a hormone which, after much controversy, has received the name of *cortin*. Other names found in the literature for this secretion are interrenin and interrenalin. Recently another hormone, cortisone, has been isolated from the cortex. Its effect on arthritis has been noted above.

The Adrenal Cortex. The cortical hormones are steroids, chemically similar to the estrogenic and androgenic hormones liberated in the gonads. Extensive experimental work has determined that the cortex is essential to life. Removal of the gland from the experimental animal results in muscular weakness, frequently in paralysis of the hind limbs, and in fall in blood pressure, and failure of the heart and of respiration.

It is known that cortin, in addition to the effects noted, plays a protective part in the intestine, apparently rendering nontoxic substances which in its absence exert harmful effects. It affects kidney function. One of the results of adrenalectomy is decrease in urinary output. It has already been pointed out that loss of the adrenals causes loss of blood sugar and glycogen from the liver, resulting in a hypoglycemia. This imbalance may be the result of the interaction of the islands of Langerhans and the adrenal cortex. The cortex is necessary for normal growth. Its physiology first became known through Addison's disease, which in-

volves a deficiency of cortical function following destructive lesions. These may involve tuberculosis, atrophy, syphilis, or neoplasms of the gland. The first results of the disease are excessive muscular weakness; irregularities in intestinal activity; heart involvement; and excessive pigmentation of the skin, causing a heavy bronzing. At present the outlook is more hopeful for sufferers of the malady. Sodium chloride with sodium bicarbonate is effective, in some instances, in maintaining the animal or individual indefinitely after adrenalectomy.

Another effect quite remote from those previously associated with the adrenal cortex occurs in hyperactivity of the gland or after prolonged injection of cortin in a growing animal. Under such conditions early sexual maturity appears. This condition sometimes appears in the human infant, when it causes masculinization of the female, *i.e.*, bearded face and male body form, while in the male it produces sexual precocity, increased libido, and sometimes a herculean body.

The cortical cells in the mammals have a characteristic arrangement into zones. The outer, nearest the capsule, is called the *glomerulosa*, because of the rounded appearance of the cell chords as they terminate underneath the capsule. This is followed by an area in which the cell chords are regularly arranged in straight clusters, the *fasciculatus*. The latter terminates outside the medulla in an irregular interwoven arrangement of the *reticularis*. It is from this last region, which includes the X zone, that the sexual activities of the cortex apparently stem.

The Adrenal Medulla. The adrenal medulla is characterized by chromaphil cells which arise, as stated, from the same elements responsible for the origin of the sympathetic nervous system. The cells are irregular in outline and marked by an extremely fine granular cytoplasm and distinct nuclei. Venous sinuses and vessels are in intimate contact with the secreting cells. A central vein, opening into the renal vein and representing the confluence of the many vascular channels in the medulla, is the chief draining vessel of the gland. The arterial blood is supplied by small, direct aortic branches as well as by twigs from the inferior phrenic artery. A curious by-pass direct from the adrenal gland to the kidney is offered by small vessels that extend directly from the gland to the kidney capsule and thence to the kidney cortex, making it possible for adrenalin to reach the kidney without first circulating through the body. The innervation to the gland, sympathetic in nature, is directed to the medulla after first traversing the cortex. It is derived from the celiac, renal, and adrenal plexuses and consists of five nonmedullated fibers and ganglia.

The secretion of the medulla, first designated as epinephrine in 1897 by

J. J. Abel and A. C. Crawford, who noted effects on the cardiovascular system of a preparation they isolated, has given way to the term *adrenalin*, by which the active extract of the medulla is known today.

The action of adrenalin is dramatic in restoring heartbeat, circulation and respiration after temporary failure, which undoubtedly would be permanent failure without administration of this excitatory agent. The late Dr. George W. Crile, one of the first to use adrenalin in emergencies arising in the operating room, stated that he and his coworkers never became accustomed to the dramatic effects of adrenalin injection, after the sudden failure of blood pressure, stopping of the heart, and cessation of breathing, in occasional serious operations. The patient, after an interval which in some cases lasted as much as 8 min., would again begin breathing, the heart would return to its regular beat, and the blood pressure increase to safe levels, with restoration of normal color. Before the advent of adrenalin, after heroic attempts at artificial respiration or stimulation, the patient who experienced sudden failure during surgery failed to return to consciousness. The short interval when signs of life are absent, to be restored by adrenalin, raises interesting problems concerning the dependence and the persistence of personality upon respiration and heartbeat, problems which cannot be explored here.

The action of the medulla has led to its designation as the emergency gland of the body. This will be better understood when its functions are examined. Adrenalin acts on smooth muscles; it inhibits certain actions and stimulates others. This apparent contradictory or unpredictable effect is analogous to that produced by sympathetic nervous stimulation. If a group of smooth muscles contract on sympathetic stimulation, they will also do so under the influence of adrenalin. If they are inhibited by nerve stimulation, adrenalin will inhibit them. Adrenalin increases the force of the heartbeat, the blood pressure, the depth and irregularity of breathing, the muscle tonus; it mobilizes sugar, *i.e.*, it speeds release of glucose from muscle and liver glycogen.

These effects of adrenalin, which may be called forth by roundabout stimulation of the sympathetic system elicited by excitation of the sensory organs, make it a true emergency gland. The eye, ear, or nose, for example, may receive an emergency stimulus. This can be shunted to the sympathetic system via the hypothalamus and the sympathetic nuclei in the spinal cord and to the chain ganglia. This stimulus, passed by the celiac ganglion to the adrenal medulla, causes an instantaneous response in additional secretion, which brings about the results on heart, vascular tree, bronchi, and so forth, that have been indicated. Adrenalin releases the constrictions of the bronchial muscles and has come

into use to relieve bronchial spasms in asthma. It produces a physiological effect in dilutions up to 1 in 500 million. The daily output of adrenalin in the human adrenal medulla is extremely minute; the entire gland contains 3 to 7 mg. of the active substance.

Closely allied in its effects to adrenalin is sympathin, a product released at the smooth muscle-nerve junction upon stimulation of the post-ganglion fibers of the sympathetic system. Walter Cannon, while not the first to postulate this humoral activity of the nervous system, was active in developing experimental proof of its existence.

Another humoral agent has been disclosed through the studies of Sir Henry Dale on the stimulating of vagal fibers to the heart and the subsequent release of a substance into the blood, perfusing the heart. Blood containing this depressor agent has the ability to depress the heart rate of another animal when passed into its circulation. This inhibitory substance resembles, or may be identical with, acetylcholine, a fact first established by Otto Loewi. The functional difference between sympathetic fibers and parasympathetic fibers is also reflected in the substances released, sympathin in the first case and acetylcholine or an agent similar to it in the second. Sir Henry Dale has suggested the terms *adrenergic* and *cholinergic* to designate the two groups of fibers.

THE GONADS AS ENDOCRINE ORGANS

The gonads are naturally associated with reproduction. The layman, unless he be a stock breeder, poultryman, or farmer, may never have linked the glands with other functions. Anyone who has observed the profound effects of castration on a stallion, a boar, a bull, or a rooster realizes that removal of the gonads causes a suppression or a failure of many of the normal male characteristics, and even some characteristics that are not necessarily confined to the male, such as bearing, behavior, *élan*, spontaneous play, and nervous peculiarities or traits. Profound although less immediately noticeable effects also appear after castration of the female, emphasizing the fact that the ovary has functions besides that of developing eggs.

THE OVARY

The ovary, from its earliest developmental stages, is provided with many potential egg cells, of which but a few will ripen in reptile, bird, and mammal, and still fewer will ever achieve their true function, which is union with a sperm cell and production of another organism (Fig. 238A). Surrounding the developing ovum in a typical mammalian ovary is a *zone of follicular cells*, arranged into a stratified epithelium

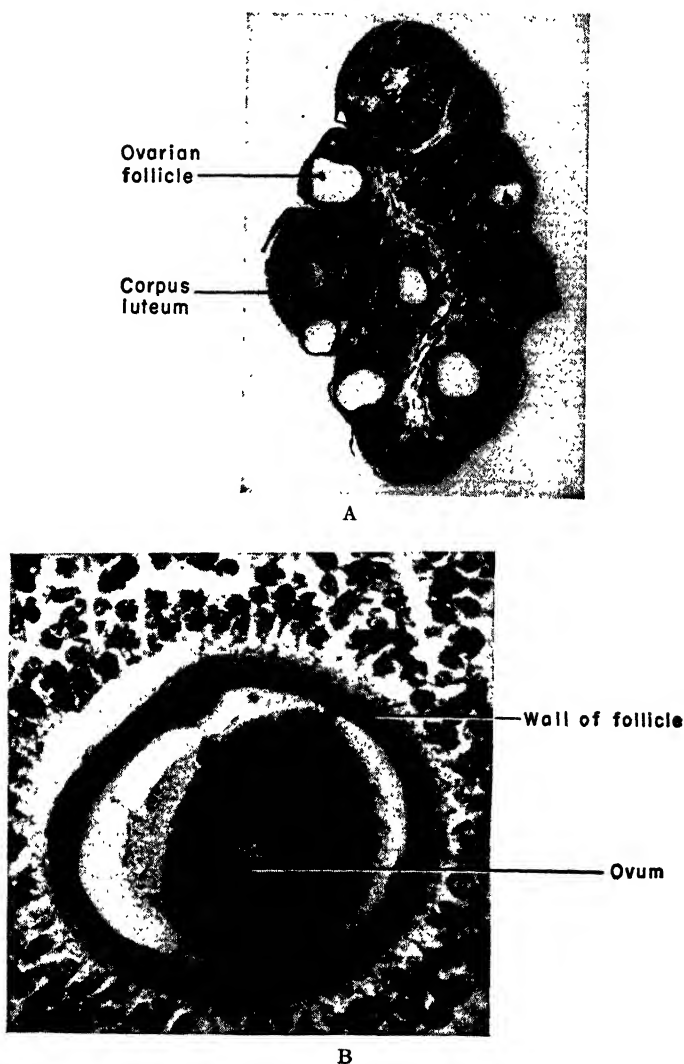


FIG. 238. *A*, the ovary as endocrine gland. The normal ovary shows small and large follicles and corpora lutea. The organ is in a constant state of change. *B*, ovarian follicle. The individual follicle surrounds the developing ovum. The cells of the follicle secrete the hormone estrin. (Courtesy of Parke, Davis and Co., Detroit.)

about the ovum as the follicle grows (Fig. 238*B*). Gradually, clear spaces appear within this follicular sphere. These spaces are filled with liquid secreted by the stratified epithelium around the follicle. On one side the follicular cells are massed solidly against the ovum, forming the *cumulus oöphorus*. The layers of tissue about the follicle are further differentiated into a *theca externa* and a *theca interna*. With these changes, *follicular liquid* is secreted and expands the follicle; the latter meanwhile is migrating toward the surface of the ovary. Assuming that the female, in whom these events happen, is in the postpuberal stage, the follicle bursts when ripe. This phenomenon, known as *ovulation*, occurs approximately on the fourteenth to the sixteenth day following menstruation in the human female. The follicular liquid is absorbed, and the ovum normally finds its way down the oviduct and into the uterus. The *ruptured follicle* retains its epithelial layer, while a small clot may form in the follicle. A follicular body, better known as *corpus luteum*, is formed by the retained follicular cells. The cells of this corpus luteum attain a considerable size and are known as the *lutein cells*. With the next menstruation, they begin to degenerate, and after a period of several months the lutein cells are completely replaced by the *corpus albicans*, composed of hyaline substance. If pregnancy follows ovulation, the corpus luteum persists during the gestation period. In the absence of pregnancy a new follicle develops, and this rhythmic cycle is repeated during the period of fertility of the female. Essentially, the same steps occur in the egg development of other mammals. In some, these changes appear only seasonally, in others, in connection with the *estrus cycle*, while in some rodents (rabbit) ovulation occurs only after copulation or after injection of estrogenic hormones.

Up to this point we have given no indication of ovarian endocrine functions or their sources. Let us examine this problem briefly. The follicular liquid secreted by the stratified epithelium surrounding the ovum contains a potent hormone *estrin*. The development of the follicle, including the follicular cells and the secretion estrin, is determined by the follicle-stimulating F.S.H. hormone elaborated by the anterior lobe of the pituitary gland (Fig. 239). Presumably before puberty this F.S.H. is liberated in amounts insufficient to cause ripening of the follicle and ovulation. As a consequence, follicles may grow to a certain stage and then involute instead of ripening.

The estrin liberated in the follicular liquid is partially taken up by the blood stream even before rupture of the follicle and stimulates the *endometrial* lining of the uterus to the formation of additional blood and glandular supply, as though in preparation for reception of the ovum.

With rupture of the follicle, additional estrin is absorbed by the peritoneum and acts on the uterine endometrium through the blood stream. With the changed status of the follicle after rupture, little or no estrin is secreted.

The transformation of the follicular cells into a corpus luteum again is not an independent ovarian activity but is determined by the action of another anterior pituitary lobe hormone, the luteinizing hormone L.H. This agent causes proliferation and enlargement of the lutein cells. This in turn converts these cells into an endocrine organ, since

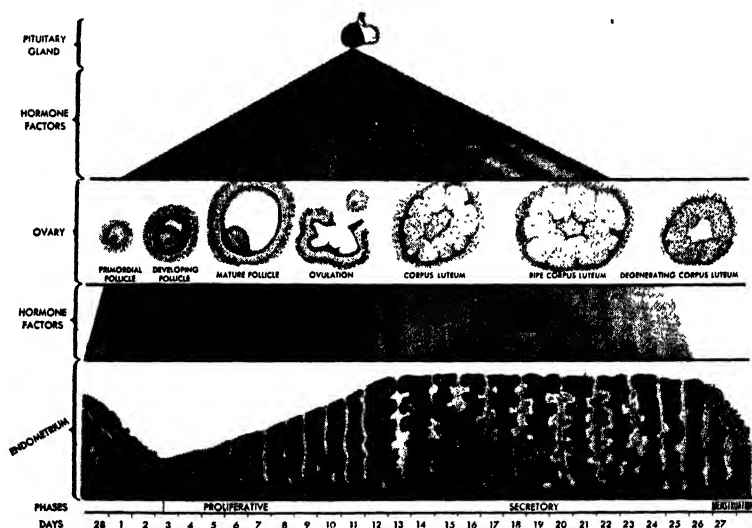


FIG. 239. Pituitary control of sexual cycle of the female. (Courtesy of the Armour Laboratories, Chicago.)

they now liberate another hormone, *progestin*. This, again acting through the blood stream, stimulates the endometrial uterine lining and causes further glandular enlargement of its characteristic corkscrew glands, as well as its increased vascularization.

As already noted, if pregnancy occurs, the corpus luteum is retained and under its influence the high degree of vascularity and glandularity of the uterus is maintained. Further, under this influence the anterior lobe of the pituitary gland appears inhibited in its ability to produce the F.S.H. in amounts sufficient to cause further follicular development. If

pregnancy does not occur, the F.S.H. apparently initiates production of another follicle and suppression of the corpus luteum. With the retrogression of the corpus luteum and the diminished secretion of progesterin, the endometrium breaks down. This breakdown involves hemorrhage and sloughing of its tissue and is *menstruation*.

It will be observed from these interrelationships that a mechanism has been perfected in the body to control the production of ova, the maintenance of the uterus, the renewal of the uterine lining, the retention of the embryo in the uterus, and ultimately the expulsion of the fetus, although all the steps determining this phase of reproduction, for example, the control of the termination of gestation, are not yet clearly known. The entire regulatory mechanism involves more than the ovary, for the latter is under the remote but effective control of the pituitary gland. Apparently no direct nervous direction over the involved cyclical phenomena is exercised. The entire complex series of events work as though directed toward the end of production of offspring. In the intervals between pregnancies, cyclical renewals of endometrium and repeated ovulations emphasize the key significance of reproduction as a means for species survival. The biological explanation for ovulation and its attendant phenomena is that through survival of mechanisms which worked effectively, to which were added mutations bringing new factors, this essential regulatory system, upon which the entire fate of the species depends, was evolved.

THE TESTES

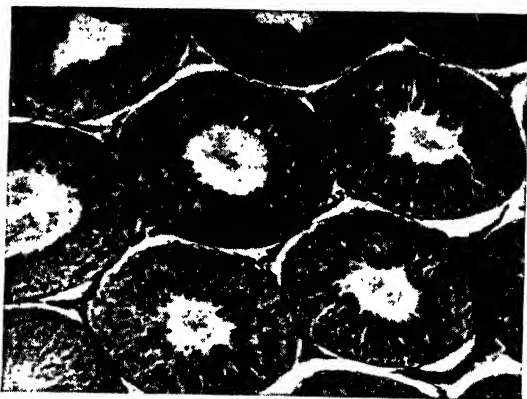
The testis is an encapsulated gland, lying outside the body cavity in many mammals (Figs. 221, 222, 240). It is a compound tubular gland, which in mammals is divided into many small lobules. The sperm-producing cells are arranged in long *seminiferous tubules*. Their structure and functions were dealt with in the description of the reproductive system (page 455). Our interest here is in the elements that may possess endocrine functions. These lie in the interstitial spaces outside the tubules. Known as the *cells of Leydig*, the *interstitial cells* are scattered loosely between the contorted seminiferous tubules. The cells are irregularly shaped, with large nuclei, some with two nuclei, surrounded by granular cytoplasm. Presumably they are modified connective-tissue cells.

Other cells in the testis, for which endocrine functions have been sought but never verified, are the *Sertoli cells*. These are sustentacular elements developed in close relationship with the spermatogonial cells.

The question has not been settled as to whether or not the spermato-



A



B

FIG. 240. A, the testes and the effect of hypophysectomy. The testes undergo marked degenerative changes after hypophysectomy. B, normal seminiferous tubules of the rat. In the normal seminiferous tubules, sperm cells occur in varying stages of development ranging from spermatogonia, spermatocytes, spermatids, and spermatozoa, in that order. (Courtesy of Parke, Davis and Co., Detroit.)

gonial cells possess endocrine functions. The fact that in cryptorchidism (retention of the testes in the body cavity) the interstitial cells may function and produce androgens resulting in virility and normal libido, while spermatozoa fail to develop, points to the likely exclusion of spermatogonia as producers of endocrine secretions.

The generic names for the secretion of ovary and testis are *estrogens* and *androgens*, respectively. The latter are administered as androsterone ($C_{19}H_{30}O_2$) or testosterone ($C_{19}H_{28}O_2$). Chemically, both estrogens and androgens are closely related to cholesterol. As a matter of fact a dehydroandrosterone has been prepared synthetically from cholesterol.

The chief role of the androgens is the development of secondary male characteristics: body form, larynx, hair distribution, penis growth, male behavior—all are under the influence of the male sex hormone. As in the ovary, the activity of the interstitial cells is determined by the gonadotropic hormone from the anterior lobe of the pituitary gland.

PLACENTA

The *placenta* is known today to possess endocrine functions. A number of estrogens presumably secreted by its cells have been collected from pregnancy urine. The *chorion*, likewise, produces a gonadotropin recoverable from pregnancy urine. It is this factor which is responsible for the success of the Friedman pregnancy test, for when urine containing gonadotropins is injected into the blood stream of a rabbit, the animal used in the Friedman test, it produces ovulation. Recently it has been found that introduction of a small amount of "pregnancy urine" (5 cc.) into the lymphatics of the male frog will cause discharge of sperm from the cloaca within an hour or two. This pregnancy test is replacing the longer and more expensive Friedman test.

This concludes the brief survey of the endocrine glands. While the account has not been approached from the comparative anatomical viewpoint and has perhaps stressed physiology rather than structure, it should place vividly before the student the complex interrelations and executive functions of these organs. The secretions of the several organs constituting the endocrine system apparently are identical regardless of the species examined.

An analysis of these several functions reveals that they serve the organism as a whole, and while at first glance the thyrotropic hormone of the anterior lobe of the pituitary gland, for example, might appear to act on the thyroid alone, the latter in turn, because of this action by the pituitary gland, serves the body as a whole. Analysis reveals further

that these glands are closely related to the direct release of energy. This holds particularly for the thyroid and adrenal bodies.

We must assume that they, like the nervous system and more than the remaining systems, help to determine the level of being a species achieves. This does not mean that sudden deprivation of thyroid or adrenal glands reduces the human being to the level of the ape. It does mean that to behave or function like a human being a particular degree of development and functioning of these glands is requisite. The cretin, for example, born with a marked hypofunction of the thyroid gland, is definitely on a lower than human plateau of performance or behavior. While structurally he may resemble the human being, functionally he falls below that level.

The human thyroid-adrenal relationship does not resemble that of the remaining primates. The apes and monkeys possess relatively large adrenal and small thyroid glands. The human pattern is the reverse of this. In man the average weight of the thyroid gland is 25 gm.; that of the adrenal 10 to 12 gm. In a gorilla of 181-kg. body weight, which the author examined, the adrenal glands weighed 35 gm. and the thyroid 6 gm. In a chimpanzee of 57 kg. body weight the adrenal weight was 8.93 gm. and the thyroid 4.85 gm.

The psychic effects of this regulating system may not be overlooked by psychologist or psychiatrist. Success or failure in life, whatever these terms may connote, are intimately associated with the normal or abnormal performance of these glands and their attendant influence upon the nervous system.

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CHAPTER 13

ANTHROPOLOGY

In the preceding chapters many references have been made to man with the assumption that his appearance in time and his growth and development were governed by the same laws that controlled other animals. The evidence for his common origin and his relationship with other animals appeared so conclusive that the evolutionary theory has been the only viewpoint of descent seriously considered in these pages. Because of his significance to himself as well as for his effects on the flora and fauna and inorganic elements of the earth, it seems desirable here to focus more definitely on his origins and trace, where possible, something of his immediate ancestry.

ANTHROPOIDEA

There are living today four genera of apes and one genus *Homo*, all of them members of the suborder Anthropoidea and of the order Primata (Fig. 241). They are further distinguished as Catarrhini, or narrow-nosed primates, in contrast to the Platyrrhini, or broad-nosed monkeys of the New World. The ape genera include *Hylobates*, represented by the gibbons and siamangs (Fig. 242); *Simia*, by the orangutans, both of these restricted to Asia (Fig. 243); *Pan*, by the chimpanzees (Fig. 244), and the genus *Gorilla* represented by the gorillas (Fig. 245), the last two native of Africa. Even a layman recognizes the close similarity between man and the chimpanzee, gorilla, or orangutan. Careful dissection reveals in addition to the external features 60 to 98 characteristics that the great apes have in common with man. Literally the resemblances extend from head to foot; from the calcarine fissure in the brain to the musculature of the great toe. While the latter is no longer opposable in man, its musculature is closely similar to that of the apes. Physiological resemblances, too, are not wanting; blood studies, for example, show an increasing compatibility between the blood of man and that of the apes. The blood of monkeys when mixed with human blood, for example, agglutinates, while agglutination does not take place between the blood of man and the chimpanzee. Susceptibility to common diseases is another feature shared by the two groups and implies close similarity or relationship.

Since the enunciation of the evolutionary theory the layman has been given a distorted picture of the biologist's viewpoint by the defenders of the direct creation theory concerning man's relations to the balance of creation and more specifically to his possible connections with the re-

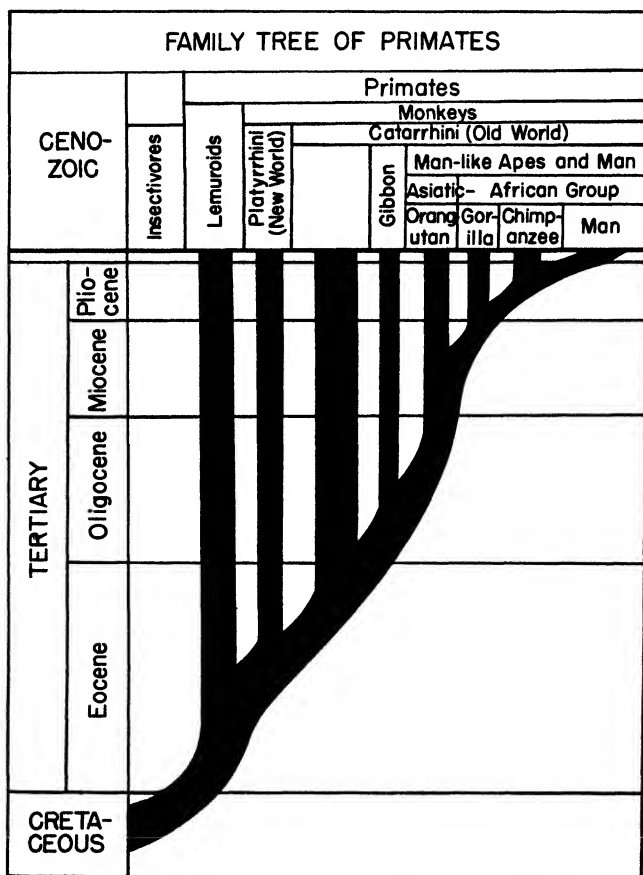


FIG. 241. The family tree of the Primates. (After von Eickstedt.)

maining primates. By posing the question, "How would you like to be descended from a monkey?" the protagonists of the direct creation theory apparently feel they have settled the question of man's descent. The answer to this problem will not be found in dialectic argument or in

heated discussion in which both sides proceed from bases so diverse that there is not even agreement upon the question as to what constitutes evidence. Biology can best proceed by continuing to gather careful evidence, which in this instance is limited largely to fossil remains or to embryological and anatomical homologies.

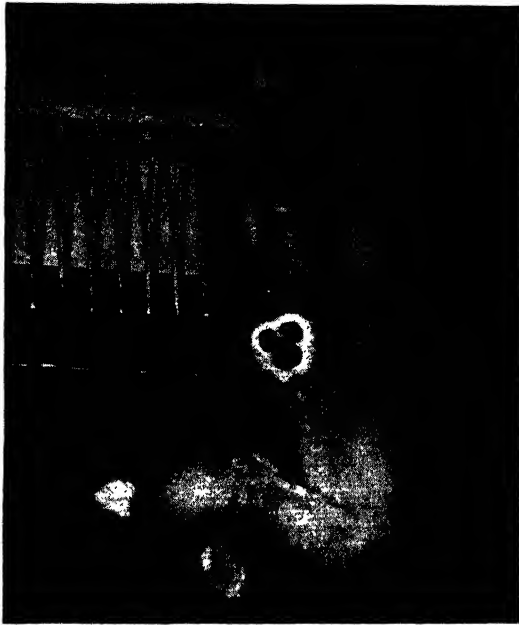


FIG. 242. The gibbon. This is an Asiatic ape with extremely long arms. It is one of the best representatives of the brachiating primates. (*Courtesy of the Lincoln Park Zoo, Chicago.*)

THE RISE OF MAN

Our immediate problem in these pages is the rise of man and his relationship to the remaining primates. What of their origin? Has man descended from any one of the four great apes? Do close relationships exist among the four, and does man represent a distinct and separate line? If we are able to approach a reasonable answer to these questions, we are still confronted with the problem of the origin of the entire group.

There is general agreement among the anthropologists that man did not arise from any one of the existing lines of anthropoid apes but that

his remote ancestors were derived from the primate stem before its then existing representatives became highly specialized. We would seek his origins not at the end but rather at the beginning of the line. The orang stock also is assumed to represent an early differentiation from the primate stem. According to Wood-Jones, the ancestral orangs were already developed in the Upper Miocene (7 million to 12 million years ago),

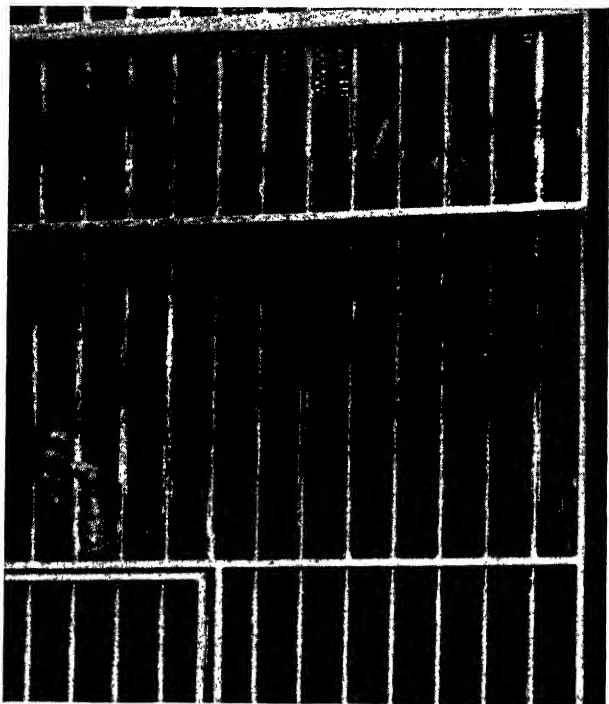


FIG. 243. The orangutan. An Asiatic ape, it is characterized by considerable sexual dimorphism. The males are much larger than the females. (Courtesy Milo Perkins, Lincoln Park Zoo, Chicago.)

presumably from a Paleosimian, Sivapithecian offshoot. The gibbon, a third derivative of the common primate stock, traces his ancestry, according to the same author, through a *Gyropithecus*, *Prohylobates*, *Pliopithecus*, and *Propliopithecus* ancestry, which carries this branch back from the Pliocene to the Lower Oligocene period, 30 million to 35 million years ago. To quote a passage from Elliot-Smith: "In the remote

Oligocene, a Catarrhine Ape, nearly akin to the ancestors of the Sacred Monkey, became definitely specialized in structure and adaptation for the assumption of the erect attitude. This type of early anthropoid has persisted with relatively slight modifications in the Gibbon of the present day." Wood-Jones believes that both the orang and the gibbon show affinities with the tailed langur monkeys of Asia, while the chimpanzee and gorilla, less specialized as brachiators than the Asiatic apes, show affinities with the guenons, macaques, and baboons. Their ancestry



FIG. 244. The chimpanzee. This is an African ape, perhaps the best known of the four great apes. It shows many close resemblances to man. (Courtesy of Ward's Natural Science Establishment, Rochester, N. Y.)

indicates descent from a *Dryopithecus*-*Paleopithecus* stock of the Lower Pliocene.

The picture we obtain in reviewing the evidence of interrelations of the anthropoid branch of the Primates is that three groups, (1) the *Prehominidae*, (2) the ancestors of the gibbons and orangs, and (3) the chimpanzee-gorilla stock, arose from a common primate stem. The last group diverged into separate gorilla-chimpanzee genera much later than did the orang-gibbon stock. Convergence following these separations led to increasing resemblances between the chimpanzee, gorilla, and hu-

man stocks, while increasing divergence occurred between the human and gibbon-orang stocks. The following analysis of resemblances taken from Sir Arthur Keith's tabulation of characteristics may be interpreted



FIG. 245. The gorilla. The largest of the apes, restricted to the Belgian Congo, may reach a weight of over 500 lb. (Courtesy Milo Perkins, Lincoln Park Zoo, Chicago.)

as verification for the view stated above. Man's anatomical characteristics are shared as follows according to this tabulation:

With the gorilla man shares 87 characteristics.

With the chimpanzee man shares 98 characteristics.

With the Old World monkeys man shares 53 characteristics.

With the orang man shares 56 characteristics.

With the New World monkeys man shares 60 characteristics.

The gibbon shares 323 characteristics with the Old World monkeys compared with only 53 which man shares with them.

In a tabulation of intelligence rating of the four ape genera which Hooton has taken from Professor Yerkes' records, the latter grades them as shown in Table 16 with relation to their nearness to man.

TABLE 16. INTELLIGENCE RATINGS OF APES

Criteria	Gorilla	Chimpanzee	Orangutan	Gibbon
Curiosity.....	2	1	3	4
Imitation.....	3	1	2	4
Teachableness.....	3	1	2	4
Attention.....	1	2	3	4
Adaptation with insight.....	2	1	3	4
Attention with foresight.....	2	1	3	?
Memory-time span.....	1	2	2	3
Imagination.....	2	1	2	3
Instrumentation.....	3	1	2	4
Adaptation of environment versus self-adaptation.....	3	1	2	4
Mechanical ability.....	3	1	2	4
Behavior adaptability.....	3	1	2	4
Psychological resemblance to man.....	1	2	3	4

It will be observed that in spite of the higher rating given to the chimpanzee, Yerkes places the gorilla next to man psychologically.

Let us turn to the problem of the Primate order. Can anthropology or comparative anatomy provide any clues to the rise of this restless group? Evidence indicates that the order arose from a primitive group of lowly insectivorous animals related to present-day tree shrews. Their tree life set apart this branch of the insectivores and by imposing new external conditions called forth adaptive responses on their part. This manifested itself ultimately in a freeing of the forelimbs, comparable in certain respects with that which is taking place in squirrels today. It was manifested also in other adaptive modifications such as increasing utilization of the clavicle and the shoulder girdle and lengthening of the latissimus dorsi muscle, attaching it to the pelvic girdle and thus knitting pectus with pelvis. It involved changes in the position of the eyes, decrease in olfactory sensitivity, shifting of thumb and great toe into apposition with the remainder of the hand and foot, transformation of claw into nail, and acquisition in some cases of a prehensile tail as an additional support in the tree. Internally, more secure anchoring of the intestine by mesenteric adhesions played hand in hand with the external changes.

These far-reaching modifications demanded vast eons of time, although the interval has been short in comparison with the great span from the

beginning of life to the coming of the first primates. Earliest tarsoids, lemuroids, and insectivores go back to the Eocene period about 45 million to 55 million years ago. Small mammals may be traced back still farther to the Cretaceous period about 100 million to 125 million years ago. The advance of these small mammals coincides with the decline of the great reptiles at the close of the Cretaceous period.

The Tree Shrew. The tree shrews Tupaiidae, a family of the insectivores, are small Asiatic mammals distributed through the Malay Peninsula, India, Burma, China, and as far west as the Philippine Islands. They are squirrel-like in appearance, with a naked nose and comma-shaped nostrils, resembling in this respect the snout of lemurs. They possess digital pads on finger and toe tips as well as four interdigital, thenar, and hypothenar cushions. The claws, present on all toes and fingers, are elongate and laterally compressed. The jaws jut forward from underneath the brain case, producing an elongate face. A prominent tympanic bulla enclosing the tympanic ring marks the floor of the mastoid bone.

The surface of the brain is smooth, with a prominent olfactory area extending beyond the cerebellum rostrally, while posteriorly the latter fails to cover the cerebellum. According to Wood-Jones there is more than mere resemblance between lemurs and tree shrews, since he recognized a number of identical features in the two groups. He goes so far as to call the tree shrews primitive lemurs and denies membership of the latter to the primate assemblage, preferring inclusion of the two groups into a single phylogenetic series designated as Strepsirhini; the primates he designates as Haplorhini.

The Lemur. The lemurs (literally ghost animals) are considered generalized mammalian forms by Wood-Jones (Fig. 246). Their fossil ancestry goes back as indicated to the Eocene period. Just where the Strepsirhini and the Haplorhini branched from a common stem is unknown. A number of distinct lemurine forms have been described. Such fossil lemurine remains have been discovered in Madagascar, apparently living at a time of what has been designated as phylogenetic riot. Divergences among the group range from specimens (*Megaladapis*) as large as donkeys, *i.e.*, larger than any living or extinct apes, with skulls some 300 mm. in length, to forms with broadened muzzles and upturned rhinaria, possibly about the size of a human being. These last lead to the belief that they may have represented aquatic adaptations. Others of these lemurine fossils lead directly to the present-day lemurs.

Living lemurs show closer affinities with the insectivores than with

any other group, and they appear linked quite definitely with the tree shrews Tupaiidae. The common likeness of the two groups includes the periotic bulla which surrounds the tympanic ring and identity in the construction of the inner wall of the orbit. As indicated, Wood-Jones considers the tree shrews primitive lemurs and separates this lemur-tree shrew group entirely from the Primates. He believes them to be progenitors of the other mammalian orders. This view, based on their existence as lemurs (*Adapis* and *Notharctus*) as early as the Cretaceous



FIG. 246. The lemur (*Lemur catta*). This animal is found both in Africa and in Asia. The snout is elongate. The lower incisors are almost horizontally directed.

period, implies that the common ancestor of the tree shrew-lemur stock extends back still further to the pre-Tertiary period, which takes us near the cradle of the mammalian order.

Some of the lemur characteristics include lower incisors directed almost horizontally; cerebral hemispheres which do not overhang the cerebellum; small frontal lobe; skull suspended from occipital condyles, the latter far back on the skull as in most lower mammals; hind limbs longer than forelimbs; four-footed stance and gait; nails except on the second digit of the foot, which is provided with a claw; arboreal and

nocturnal habits; two or three offspring at a birth, with which is associated an additional pair of nipples in the groin. Existing lemurs are small, ranging in size from mouse to cat; they are omnivorous in food habits and possess a fox-like snout. Hooton places them under the sub-order Lemuroidea below the Tarsioida and Anthropeidea, which constitute the remaining orders of Primates.

They appear, then, to represent an early branching from a common tree shrew-lemur stock, and thus while they share many features with the true primates, the line of the latter apparently does not pass through the lemur division. Tarsius, on the other hand, a small mammal about the size of a rat, is placed with the monkeys, apes, and man in the super-order Haplorhini (Fig. 247). The terms *Haplorhini* and *Strepsirhini* refer to the type of nose and its relationship to the upper lip; the Strepsirhini, as pointed out, have a naked, primitive rhinarium and nonprotrusible upper lip; in the Haplorhini the naked skin is restricted to the region immediately around the nasal opening, and the upper lip is protrusible.

The Tarsius Monkey. The tarsiers have many more features in common with the Anthropeidea than the lemurs. They constitute a single family with the same general Asiatic distribution as the lemurs, although they do not occur in Africa and Madagascar as do the latter. The upper lip is hairy in contrast to the naked upper lip of the lemurs; the eyes are very large, a modification correlated with their nocturnal habits. Digits and palmar and plantar surfaces of hands and feet are provided with digital and interdigital pads. Nails occur on the digital tips with the exception of the second and third toes of the foot, which are armed with sharp, curved claws employed for grooming. Hind limbs are longer than forelimbs.

The Tarsioids represent a specialized group, adapted to night life; the skull, relatively shorter than that of the lemurs, has enormous orbits as its most conspicuous features. The tail has 18 to 23 caudal vertebrae; tibia and fibula are fused. The brain, quite smooth and modified in shape and function by the enormous eyes, carries a calcarine fissure, typical of the primates, on the medial margin of the cerebrum and a sylvian fissure on its lateral surface.

With reference to its position in the primate scale, Wood-Jones states, "It is agreed on all hands that the monkeys and apes arose from the Tarsioids of the Eocene or pre-Eocene and that Tarsius is a living and very little modified Tarsioid. . . . It seems a pity not to accord to the living Tarsius what would have been accorded to it if it had not survived the Eocene—its right to be included among the Anthropeidea or Pithe-

coidea." Hooton, on the basis of the anatomical evidence, believes "there is good reason for supposing that the higher developments in the Primate Order have occurred through the advance of a group of tarsioide ancestors." He holds that man's place in the Primate order must be sought beyond the Lemuroidea and Tarsioidea. So much for the two



FIG. 247. Tarsius. The specter monkeys are Asiatic in distribution. They are small, adapted to night life. Claws occur on the second and third digits of the foot; nails appear on the remaining digits. (Courtesy of the Philadelphia Zoological Gardens, Philadelphia.)

earliest primate stocks. Let us consider briefly the derivation of the Anthropoidea.

Parapithecus. Small primitive anthropoids (Parapithecus) had already made their appearance in the Oligocene period (about 35 million years ago) along with the ancestors of the Old World monkeys. This was the result of a great expansion of the tarsioide in the Eocene (about

54 million years ago) when they deployed over the Old World as well as the New. In the latter they gave rise to present-day platyrrhine monkeys and marmosets with characteristics peculiar to themselves. In the Old World; the present-day catarrhine monkeys, presumably derived from a tarsoid group and represented by a fossil monkey *Parapithecus*, expanded and diverged into the *Cercopithecidae*. Either parallel with or somewhat later than this development of the Old World monkeys from *Parapithecus* occurred the separation of the anthropoid-human stock from *Propliopithecus*, the first anthropoid, whose fossilized remains have been unearthed in Fayum, Egypt.

Propliopithecus. *Propliopithecus haeckli* dates back to the lower Oligocene, which means that it existed about 30 million to 35 million years ago. Its lower jaw, which constituted the find, with teeth complete but with jaw rami missing, had a tooth row but 31 mm. long in contrast to that of a modern gibbon, the smallest of present-day apes, where it is 51 mm. in length. *Propliopithecus* probably gave rise to another ape, represented by a small fossil, *Pliopithecus*, which in turn is believed ancestral to the gibbon. The orang is thought to be derived from a Paleosimian anthropoid, already differentiated in the middle Miocene (about 18 million years ago). Still another group, *Sivapithecus*, in the upper Miocene, presumably an offshoot from Paleosimia, led to *Dryopithecus*, which presumably gave rise to the chimpanzee and gorilla genera.

Dryopithecus. Remains of this later ape, *Dryopithecus*, have been recovered in Africa and in the Siwalik district of northern India. Similarities in the molar pattern of modern and fossil man with that of *Dryopithecus* leads some palentologists to believe that *Dryopithecus* represented the common ancestral stem for man, chimpanzee, and gorilla.

Proconsul africanus. *Proconsul africanus*, a large fossil ape, represented by several jaw, tarsal palate, and facial fragments, found by Leakey in Kenya, East Africa, may according to Hooton represent an ancestral line leading to man. Hooton believes it probable "that the ancestral chimpanzee line may have diverged from the main giant primate stock before the differentiation of the more specialized *Proconsul* form in early Miocene times," while the gibbonoid stock may have derived from another lower Miocene fossil, *Limnopithecus*.

Australopithecus. The next important discovery from the standpoint of man's possible antecedents also comes from Africa (Fig. 248). This discovery, a fairly complete skull and brain case, designated as *Australopithecus africanus*, goes back either to the Pliocene or the lower Pleistocene age, between 1 million and 6 million years ago. It has a number of features linking it with a group of infrahuman fossils of South Africa

extending to the Pleistocene. Since the fossil is that of a young specimen perhaps five years old, too much faith may not be placed upon skeletal resemblances with modern adult apes or man. Its cranial capacity, which was estimated at 520 cc. by Raymond A. Dart, who first described it, is greater than that of modern adult chimpanzees. The adult *Australopithecus*, whose cranial capacity has been estimated at 518 to 733 cc., would be rated above any existing apes, although its cranial capacity



FIG. 248



FIG. 249

FIG. 248. Skull of *Australopithecus*. *Australopithecus* was probably represented in Africa in the lower Pleistocene age as a subhuman pygmy race. Recently a number of finds of this race have been reported from South Africa. (Courtesy Ward's Natural History Establishment, Rochester, N. Y.)

FIG. 249. *Pithecanthropus erectus*. This race goes back to the middle Pleistocene age about a half million years ago. A number of fossil remains of this genus have been unearthed, leading to the belief that this prehuman race had a wide distribution and that it was represented by a number of species. (Courtesy of Ward's Natural History Establishment, Rochester, N. Y.)

is less than the estimates given for *Pithecanthropus erectus*. Evidence is accumulating that *Australopithecus* represented a pygmy prehuman race.

Pleisanthropus. Africa is the site of still other ancestral candidates to the human genus. Dr. Robert Broom of South Africa discovered in 1936 a fossil skull and cranial cast which he named *Pleisanthropus transvaalensis*, and in 1938 another fossil was given him which he termed *Paranthropus robustus*. These skulls bear resemblance to the orang as well as to man. The cranial capacity of the first has been estimated at 430 cc., that of the second at 600 cc.

Sinanthropus. There is a resemblance in size between the premolar dentition of the African Pleisanthropus and early Chinese man, Sinanthropus. Both Pleisanthropus and Sinanthropus possess molars with two roots instead of three as in the apes. According to Hooton the lower premolars of both indicated a stage between Dryopithecus and early fossil human types. The conical cusps of the upper molars of the South African fossils differ from those of the gorilla and chimpanzee where they are sharply pitted. In the former the conical cusps wear down evenly, as in man.

Gregory and Helman hold that the South African man apes originated "from the Dryopithecus-Sivapithecus stock of the late Tertiary of Asia and Europe and are both in a structural and genetic sense the conservative cousins of man." Hooton believes that, although much closer to man than any present or past subhuman forms so far discovered, these Pleistocene apes lacked the characteristically human brain overgrowth and that consequently they remained apes in spite of their humanoid teeth.

Pithecanthropus. The discovery of a skullcap, a femur, and three teeth of a fossil ape by DuBois in 1891, in the island of Java, renewed interest in the antecedents of man (Fig. 249). Coming at a time when the Darwinian evolutionary theory was still subject to constant attack, the discovery was well timed to support those who held that man had evolved from lower forms. Such a find could not well be explained in terms of the theory of direct creation. It could not be dismissed as a pathological specimen, nor did the catastrophic theory of Cuvier adequately account for it. This fragment, to which the name *Pithecanthropus erectus* has been attached, consisted, as noted, of a skullcap, three teeth, and a thighbone. The skullcap was low, vaulted, and ape-like in appearance; the supraorbital ridges extend as a heavy bar across the frontal bone. The brain volume has been estimated at 914 cc. The femur is slender and human in its proportions, leading to an estimate by DuBois that the individual was about 5 ft. 8 in. tall. The teeth found with the other remains later were shown to be those of a fossil orangutan.

Subsequently, additional remains of Pithecanthropus and his near relatives have been unearthed, so that today they form the nucleus of early human types from which the anthropologists appear to draw inexhaustible conclusions.

Gigantopithecus. A Chinese giant man, *Gigantopithecus blacki*; a Java giant, *Meganthropus palaeojavanicus*; the robust ape man, *Pithecanthropus robustus*, also a giant type, are among the later finds. Dr. G.H.R. von Königswald found that the giant and robust ape man fragments of the Pithecanthropus race indicate an erect posture because of

the forward position of the foramen magnum and the nature of the occiput.

In addition, von Königswald obtained three fossil teeth of *Gigantopithecus blacki* in China. These three teeth are larger than any human or living anthropoid teeth. The third lower molars of *Gigantopithecus* have a mass about six times larger than those of modern man and three times larger than the largest anthropoid or fossil human teeth.

Weidenreich believes that this giant race may have lived in India and later in China. He traces the lineage from *Gigantopithecus* through *Meganthropus* to *Pithecanthropus robustus*, *Pithecanthropus erectus*, *Homo soloensis*, *Wadjak man*, and thence to the modern *Australian*. Such lines of possible succession must be considered as extremely tentative, since the evidence is entirely insufficient upon which to build solid conclusions concerning the specific steps in the immediate evolution of modern man.

Another early human race already mentioned, showing great advances over *Pithecanthropus erectus* in its approximations to modern types, was discovered by Davidson Black in China in 1929, antedating the finds of von Königswald. This new genus of man has been designated as *Sinanthropus pekinensis* and is attributed to the middle or lower Pleistocene, which places it within a time range of about a million years ago. Fragmentary remains of some 38 individuals had been uncovered by 1938. These were represented largely by tooth, jaw, and skull fragments. The collection includes bits from young skeletons up to 14 years of age; three of individuals under 30 years; three between 40 and 50; and one of an old woman. The average cranial capacity was about 1,075 cc. as compared with an average of 860 cc. for the *Pithecanthropus* race and about 1,350 cc. in present-day man. Weidenreich believes this fossil Chinese man ancestral to modern Mongoloids because of a number of features shared by their skeletons.

Eoanthropus. *Eoanthropus dawsoni* is the name given to a human race living in England in the Pleistocene or late Pliocene period. Fossil remnants were unearthed by Charles Dawson, an English lawyer, near Sussex between 1909 and 1915. The first group consisted of nine skull fragments together with nasal bones, parts of a lower jaw, and a canine tooth. A second lot, found in 1915, included two skull fragments and a molar tooth. Other fossils of Pliocene animals as well as crude stone implements and primitive flints were associated with these human fragments. Piltdown man is believed to have lived early in the glacial period. The cranial capacity has been estimated anywhere from 1,070 to 1,500 cc. A recent estimate of Sir Arthur Keith, based upon a second reconstruction of the brain case, indicates a cranial capacity of 1,358 cc.

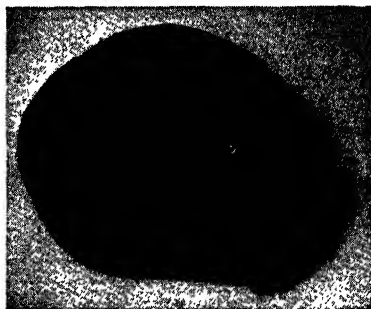
A number of additional prehuman and early human skeletal fragments

which have enabled anthropologists to reconstruct a part of the more recent human racial story have been found from time to time.

Heidelberg Man. In 1907, in the Maurer sands near Heidelberg, Germany, a well-preserved lower jaw was unearthed. This, while human in its general appearance, shows enough differences compared with the modern to classify it as a prehuman type. The jaw is broad and massive and carries characteristic human dentition; a chin is absent. With it were found skeletal remains of the Etruscan rhinoceros and elephant, long since extinct in Europe. It has been placed geologically in the second interglacial period and probably represents a forerunner of the Neanderthal race, which reached its climax in the fourth and last glacial period.



A



B

FIG. 250. *A*, the Heidelberg jaw. *B*, Neanderthal man. This race, which inhabited Europe in the last ice age, seems to have disappeared quite suddenly with the advent of Cro-Magnon man. (Courtesy of Ward's Natural History Establishment, Rochester, N. Y.)

Neanderthal Man. *Neanderthal man*, a later arrival than the Heidelberg race, was not large of stature; his height probably averaged less than 64 in. (Fig. 250). His head was massive, and his cranial capacity exceeded that of modern man. The face was large and of prognathous type. Heavy eyebrow ridges, large nasal bones, wide nasal aperture, prominent jaws, and receding chin and forehead were features quite unlike those of modern man. The eye sockets also were relatively larger, their capacity being about a third greater than those of present-day types. A canine fossa over the roots of the canine teeth, and present in modern man, was wanting. Von Eickstedt points out that the relative smallness of the zygomatic arch and other bony markings for attachment of facial muscles indicates only a small degree of activity of these muscles

of facial expression. Combined with these features, however, was a great development of the muscles of mastication.

The posture was only semierect, and the massive head was not balanced on the spinal column but was pushed forward and supported by heavy neck muscles. Arms and legs were moderately long. The head of the humerus, relatively large, probably had greater freedom in circumduction and rotation than that of modern man. Presumably in time this race diverged into subraces, *e.g.*, *Krapina man* and *Palestine man*. Evidence indicates that the race was widespread over western Europe in the last ice age, probably extending to North Africa, Asia Minor, and



FIG. 251. Cro-Magnon man. This race was modern in characteristics and became the dominant European type with the recession of the last ice age some 20,000 years ago. (Courtesy of Ward's Natural History Establishment, Rochester, N. Y.)

Asia proper, since remains have been recovered from more than 30 sites ranging from Europe and northern Africa to the Volga River.

For thousands of years, some estimates run as high as 150,000 years, this race lived more or less protected from encroachment until replaced by aggressive hunting tribes penetrating into Europe from the East with the recession of the fourth ice sheet.

Aurignacian and Cro-Magnon Man. The new races that penetrated from the East included the *Aurignacian*, or Brunn, followed by the *Cro-Magnon* (Fig. 251). To these were added a few Negroid elements which presumably came to the northern shores of the Mediterranean, represented by *Grimaldi man*, and an Eskimo-like fraction, *Chancelade*

man. These were all more highly specialized groups than the Neanderthal race they displaced, and with gradual climatic changes in Asia and Europe following the last ice age they deployed freely to the west.

Racially they are distinct from Neanderthal man, and the Cro-Magnon fraction leads directly to modern types. The Aurignacian race, characterized by small stature, primitive facial anatomy, heavy eyebrow ridges, and receding forehead, shows similarities to the living Australian aborigines. Whether any mixing occurred between these new entering races and Neanderthal man is a question not yet satisfactorily answered. Generally at the contact zone where two different races meet, there is interbreeding. Where, however, the physical differences are as great as those between Aurignacian, Cro-Magnon, and Neanderthal, it is problematic whether interbreeding was sufficiently widespread to affect the physical characteristics of later Cro-Magnon man. In this connection speculations appear from time to time suggesting that our population contains some of these ancient paleolithic remnants, although this is difficult either to verify or deny, since convincing proof cannot be offered.

The Cro-Magnon race is identified from a very large number of finds. It was tall of stature, averaging approximately 72 in. for the males; broad and short of face and jaw with well-developed chin, it had prominent cheekbones, high, narrow nose, long head, and high forehead. The heavy eyebrow ridges of Neanderthal and Aurignacian man have disappeared. This race became the dominant European type, and modern man is continuous with this line. It reached a high cultural level as evidenced by the tools, flints, and cave drawings.

The racial connections among Neanderthal, Aurignacian, and Cro-Magnon races may be visualized as follows, to paraphrase von Eickstedt. From a purely morphological viewpoint, Neanderthal, Aurignacian, and Cro-Magnon represent three developmental steps extending along the sequence from an early prehuman to a highly human status. They are three layers washed into Europe and lodged more or less over one another, mixing, interdigitating, and merging to a small degree. The original site for their differentiation must be sought elsewhere, somewhere in the east or southeast in a wide circle about the high Asiatic pole, their original homesite. Here they lived even after Neanderthal man had already spread over Europe. Biologically and geologically it is illogical to consider Europe as the center from which they radiated. Both for mankind and for the animal world the great continental mass of Asia has always been the formative center, though this opinion might be modified in the light of recent African finds.

Grimaldi Race. In the early Aurignacian layer at Mentone, two skeletons of Negroid character, the *Grimaldi race*, have been unearthed, indicating perhaps a weak deployment of the Negro from Africa into southern Europe. This race never gained a firm foothold in Europe. In similar manner Eskimo-like skeletal remains from Chancelade and Le Roc in France point to the presence of this distinctive group in a post-glacial period which was characterized by arctic flora and fauna. It appears plausible that a people adapted to tundra and steppe life would find its way into a belt which for a time was subarctic in nature.

The further pursuit and deployment of races are far beyond the scope of this chapter. We have left unanswered the question of the original homesite of man as well as the problem of the factors that led to his dispersal.

The high plateau of Asia is most frequently indicated as the original homesite. A number of factors lead to this opinion; most domestic animals have originated there; it represented the greatest single land mass offering sufficient food for great numbers of animals. Pathways lead from this great area to Europe in the west; to India and Africa in the south and southwest; to eastern Asia and America to the east. These pathways must be considered as open land areas, prairies, and savannas, which from time immemorial have been the favorite hunting and settling grounds of man.

It is assumed by some anthropologists that the differentiation into the three great modern races, the Mongoloids, the Negroids, and the Euro-poids, or Caucasians, occurred in this central Asiatic plateau. The separation into the three groups is attributed to the geological features of the area (Fig. 252). During and between the ice ages, two great barriers, the Irano-Himalayan Mountain range, crossing Asia from east to west, and the Tienio-Altai, extending diagonally to the northeast from its junction with the Himalayan, permitted this differentiation to become more marked in the many millennia at the disposal of the forces molding man.

Dynamic pulsations within the groups pushed to the periphery weaker subgroups that were emerging. These dynamic pulsations were represented by marginal groups that exerted pressure and that in turn were pressed upon by the basic types nearest the racial pole. Thus further specializations appeared within each of the three great racial groups (Fig. 253). Basic to the success of the experiment were the great climatic pulsations; glacial periods carried the groups farther afield; inter-glacial intervals permitted consolidations of gains and adaptations to the new conditions.

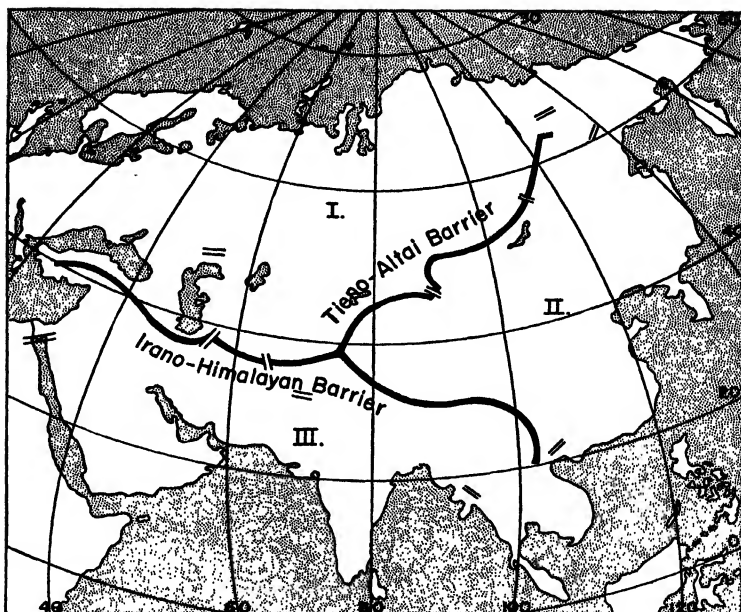


FIG. 252. Land barrier in relation to racial dispersal. The Tienso-Altai and the Irano-Himalayan barriers were effective agents in the segregation and the dispersal of the three modern human races. (After von Eickstedt.)

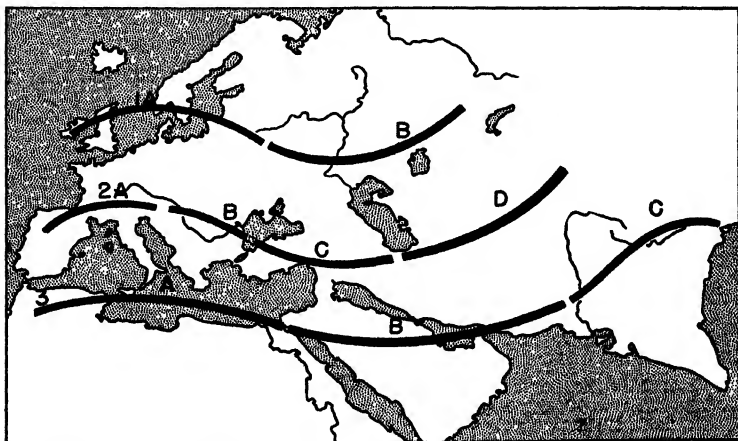


FIG. 253. The dispersal of modern European types. 1A, Nordic; 1B, East Europoid; 2A, Alpine; 2B, Dinaric; 2C, Armenioid; 2D, Turanid; 3A, Mediterranean; 3B, Oriental; 3C, Indian. (After von Eickstedt.)

The mountain barriers effectively directed the deployment of the three races. The Mongols could move to the north or south, since they were on the eastern side of the Tien-Altai range; this led them finally to the New World. The Negroes, hemmed in from the north, could push to the southwest and the southeast, thence to Africa and to a lesser extent to the southeast (the Philippines, Andaman Islands). The European stem from their vantage point could follow the western pathways to Europe.

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CHAPTER 14

FUNCTIONAL ANATOMY

Biological Speculation. In a study devoted to animal structure, with some emphasis on function, the biologist, never far from his facts, must confine himself largely to their recital; yet the biologist has every right to draw inferences from these facts, since biology is not a mere catalogue of events, nor is it confined to a description of animal bodies. It has expanded from these beginnings as a descriptive science to a science that includes natural philosophy in a true sense, into a discipline that not only employs exact measurement but that on the basis of such measurement expresses relationships in mathematical equations. One may liken a biological subject, once it is accurately expressed in such an equation, to a chemical compound after it has been refined to a crystalline state. Having established it in this form, the chemist is reasonably sure of its structure. In like manner, when the biologist expresses growth relations, for example, by equations that fit the data, he may feel confident that he is on firm ground. That does not imply, however, that a formula accurately and completely describes life.

The biologist speculates about the facts at his disposal, not in an idle, daydreaming manner, but as the result of constant occupation with his material. If he is not curious about biological facts and their implications, he should not choose biology as his field. Concerning the origins of life, he can only theorize; to date he has not been able to manufacture life in a test tube, and it is not likely that he will do so in the near future. About all he can say concerning this problem is that the chemical elements possess certain qualities which, when combined in certain proportions, under conditions which prevail on earth, are capable of forming combinations which move, breathe, and live. Further, they are able to repeat or reproduce themselves. In this building up of chemical elements, the combinations make use of oxygen and of other chemical elements in complex organizations that we call carbohydrates, proteins, and fats. These chemical combinations, when organized as animals, use these carbohydrates, proteins, and fats to build up their own bodies and utilize the energy that may be derived from them when united with oxygen. They spend this energy in producing movement and work, largely in connection with their self- or species maintenance.

Energy Utilization. Not all physicochemical combinations designated as animals reside at the same level of energy utilization or energy expenditure. In the course of time, change has come over many groups, and change continues to be evidenced in their anatomies. In the preceding chapters we have been concerned largely with the orderly nature of these changes that resulted in more than a million species of animals alone. By emphasizing their structural nature, however, we have frequently overlooked the profound changes in functions that accompanied architectural modifications.

TABLE 17. RELATIVE SPEED OF ANIMALS

Name	M.p.h.	Body wt.,* lbs.	Name	M.p.h.	Body wt.,* lb.
Cheetah.....	70	30	Kangaroo. . . .	30	130
Gazelle (Gobi)...	60	80	White-tailed deer	30	130
Antelope. . . .	45	110	Buffalo . . .	30	1,800
Jack rabbit	45	5	Stag (hunted). .	25	150
Elk (maximum short distance)...	45	200	Rabbit	25	3
Race horse . . .	40-42	1,000	Elephant (charg- ing).	24.5	7,000
Wild ass	40	300	Fox	20	12
Greyhound . . .	36	22	Dogs (various)...	20	10-30
Mongolian wolf...	36	30	Pig	11	90
Hare.....	35	4	Porcupine (driven).	2	3
Coyote	31	25	Tortoise	2.5	3
Emu	31	110	Rhinoceros.. . .	30	2,000†
			Hippopotamus. . .	20-30	2,800†

* Estimated.

† Author's data.

In the following pages we shall attempt to show briefly some of the changes in the degree of development of certain key systems and by implication associate the widened range of activities of certain animal groups with the evolution of these organs. As a preliminary to such an analysis we may cite briefly a somewhat similar but highly restricted approach, in this instance a comparison of the speed of various animals, correlated with bodily structure. These relations were described by Maurice Burton in Vol. 211 of the *London Illustrated News*.

Speed of Animals. In this contribution, entitled "Speed on Land," Burton points to a number of pertinent factors that determine the speed of animals. In the bird and fish, streamlining is of extreme importance; on land, length of leg. He compares, for example, the African cheetah, the fastest land animal, with the leopard. Although of the same body

shape, the cheetah has longer legs in proportion to its body length. Lightness of body also plays a part in determining speed but is not the sole factor, for the antelope of approximately 110 lb. body weight is as fast as the jack rabbit at approximately 5 lb., and a thoroughbred race horse at 1,000 lb. almost equals this speed. The character of the food, whether vegetable or flesh, again does not appear to be a determining factor for speed. Herbivorous animals carry a heavier load of food than do the carnivores. The herbivorous rhinoceros weighing some 2,000 lb. is as fast as the carnivorous Mongolian wolf at approximately 30 lb. The author determined the speed of the rhinoceros at slightly over 30 miles per hour while it was pursuing a truck.

The tabulation of Burton, shown in Table 17, has been modified to include the approximate body weights of the animals in question and the estimated speeds of the rhinoceros and the hippopotamus.

Inferences. Taking these figures at their face value a number of inferences may be made:

1. Size and speed are not necessarily correlated.
2. Adaptive mechanisms must be present in these animals which cause the heart, muscles, and respiratory tract to respond to increased need for blood and oxygen.
3. All these animals are within a body-weight range that permits sufficient heat dissipation from the surface and respiratory tract during rapid locomotion to avoid overheating or heat death.
4. Some animals are adapted for short outbursts of energy; others can maintain a high rate of speed over a prolonged period of time.
5. In spite of the additional food load carried by the herbivorous animals, they hold their own in the race with the carnivores.

Alligator and Lion. Another approach, alluded to in the opening chapter, involves the comparison of certain systems in the alligator and the lion. In this comparison, for example, we might have confined ourselves to a listing of the various weights, some observations on metabolism, habitat, nature of skin, and other anatomical data and concluded the problem. As living active animals, however, they excited the author's interest, and he could either dismiss them as mysteries or, in attempting to explain the source of their actions, examine those systems which he knew affected metabolism. Here again certain conclusions have been drawn, based upon an objective comparison:

1. The animals are capable of movement.
2. The lion has longer legs than the alligator; hence it is possible that it moves faster.
3. Both animals have eyes; gross examination does not tell us whether they see equally well.

4. Both animals have snouts; again we cannot tell grossly whether their olfaction is equally acute.

5. Both animals have strong jaws and teeth, indicating that they may capture food.

6. With these jaws are correlated strong bodies.

7. Both have about the same amount of muscle and skeleton.

8. The lion has limbs adapted for clawing and killing, which implies a series of new functions in comparison with the alligator.

9. With a thermometer we may determine that one is cold- and the other warm-blooded.

10. From chemistry we know that each degree rise in temperature (centigrade) speeds a chemical reaction by 10 per cent (Arrhenius formula); hence we would expect faster metabolic changes in the lion, other factors remaining equal.

11. The muscle of alligator is pale; that of the lion is red.

12. This (11) implies that the lion has a larger blood volume than the alligator.

13. Examination reveals that the heart of the lion weighs 1,175 gm.; that of the alligator weighs 375 gm.

14. Examination of the brain reveals that the lion's brain weighs 263 gm.; the alligator's, 14.08 gm.

15. The thyroid gland of the lion weighs approximately twice that of the alligator.

16. We know that thyroid gland secretion governs metabolism, and, finding the thyroid cells in the two animals of equal size, we conclude that the lion, aside from the temperature and blood volume advantage, has a higher metabolism than the alligator. This we may verify by actual measurement.

In other words, we may compare any two animals system by system and, on the basis of the combined development of all systems related to energy release, arrive at conclusions that have a high degree of validity. These permanent differences between animals of different classes, or between different species, or even between individuals within a single species have led the author to use the expression *levels of being*. This term implies, and the findings bear out the implications, that such differences fall into regular categories.

A further example of this comparative approach to functional anatomy is offered in the following résumé of a study based upon an examination of the organ weights of 3,690 animals (Appendix). For our present purpose the findings on the brain, thyroid gland, adrenal bodies, and heart only are reviewed. Further investigations are necessary to determine finally some of the inferences drawn from the data, but it is hoped

that they point the way to a functional approach to comparative anatomy and that they may lead the student to recognize the essential union of structure and function.

A Comparison of Certain Organs in Various Vertebrate Classes. It becomes apparent when one examines the brain, thyroid gland, adrenal bodies, or heart, for example, in the various chordate classes, that these glands have been subjected to an evolutionary process just as have been the digestive, skeletal, and muscular systems.

The above-named glands may be looked upon as adaptive devices which enable their possessors to modify their physical and psychic behavior at a moment's notice. They may change the rate of energy expenditure, *i.e.*, the rate of oxidation, the heart rate, the heat output, the rate of breathing and the time required for the nerve impulse to activate the organ and the latter to throw its hormones into the blood stream, if it happens to be a ductless gland. Concomitantly such action may produce secondary effects upon the nervous system which we in ordinary language call "nervousness," which state is marked by keener sensitivity, rapid response, increased muscle tonus, emotional excitement. At the basis of this there appears to be increased oxidation in the cells of the central nervous system itself. This increased oxidation is apparently due to increased permeability of the nerve-cell membranes. This is reflected in a more rapid electrical oscillatory rate of electrical potential.

The adaptive nature of these developments in the executive glandular and nervous system might imply a development or evolution toward definite ends. Undoubtedly the evolutionary process points to very definite ends, but these ends may be more apparent than real, and it is possible that they merely reflect the operation of the principle of the survival of the fittest. Nature generally is quite prodigal in scattering her seeds; she permits reproduction of a species on a grand scale without concerning herself directly with the subsequent effects of this prodigality. Under the principle of pitiless competition, those individuals in a species or those species best endowed to meet the vagaries of a changeable environment persist; those not so endowed face ultimate extinction. The operation of this principle may well account for the adaptive devices built into the bodies of existing species. Given a means of finding a foothold in the body, and there is such a means in the mutation principle, these glands, starting from unsuspected beginnings, ultimately wrest a large measure of executive control from the nervous system.

It is from this viewpoint that we speak of a scale of being in Nature; it is from this viewpoint that we account for the ascendancy of the

mammals; and it is from this viewpoint that we would explain the supremacy of man.

In an attempt to determine what if any regularities existed in the rise of brain, thyroid, adrenal bodies, and heart from fish to man, the author made, several years ago, a study of the weight relations of these organs in the different classes. It became apparent from an examination of the data that an orderly rise occurred in the degree of cephalization (brain development) and thyroid, adrenal, and heart development. The animals generally that we consider to be highest in the scale of development also show the highest degree of cephalization, thyroidization and vascularization. While the layman might have predicted such a finding, an attempt to show in mathematical form the truth or falsity of this concept has only recently been made.

Brain. Figure 254 expresses the degree of cephalization in various vertebrates. It will be observed that man leads the group by a large margin. This is due primarily to the great development of his cerebrum, although curiously the Cetacea also show a considerable development of this division of the brain. Studies of relative brain size within the human species extend back to the early days of comparative anatomy.

It is well known that the normal human brain may vary in weight from 1,000 to 2,200 gm. and that brain weight and intelligence are not necessarily correlated within these weight limits. When the weight of the adult brain falls much below the lower level, the condition may be correlated with subnormal intelligence. There are racial differences in brain weight just as there are other more obvious differences. However, just because the Eskimo as a racial group has the largest brain of any existing race, it does not imply that this race is also the most intelligent.

On the basis of the cephalization chart it will be observed that the reptiles and amphibians present a lower level of cephalization than do the fishes. From our observations it appears that aquatic life has associated with it, and perhaps requires, a larger brain than does cold-blooded land life.

Among the fishes the cartilaginous sharks are on a higher cephalization

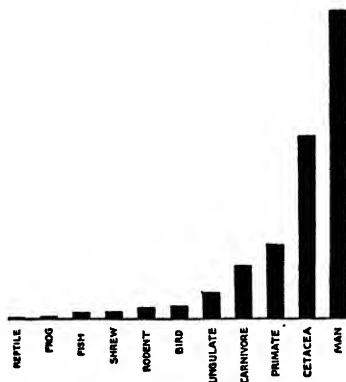


FIG. 254. The cephalization scale.

level than are the bony fishes. Among the reptiles, snakes stand at a lower level than do alligators and lizards. Among the birds the common fowl and ostrich appear at the bottom rung of avian cephalization, while the small carinates, as well as the larger pelican and the crow, appear near the top.

A comparison of brains from cat-like carnivores with the dog-like indicates that the latter possess a higher degree of cephalization, while aquatic carnivores, like seals and walruscs, are on a much higher level than either of the other two groups.

In similar manner, comparison of odd-toed with even-toed ungulates shows greater cephalization in the odd-toed than the even-toed. Just what influence this has on their mode of life, their speed, or their chance of survival is difficult to state.

In the present state of our knowledge, it is difficult to assign specific causes for these differences or to visualize the direct effects, if any, resulting from these differences. It becomes obvious, however, as was pointed out in the opening pages, that there has been a steady rise in the degree of development of the brain, just as there has been in other organ systems, and it is obvious also that the brain of warm-blooded animals is on a higher performance level than that of the cold-blooded. Further, man's large brain sets him apart from all other animals.

Thyroid Body. Applying this same method of study to the thyroid gland, we observe, in comparing the cephalization and thyroidization graphs, a curious similarity of pattern in the rise of the thyroid gland, for the last five groups represented in the diagram occupy the same relative position they do in the cephalization chart (Fig. 255). Aside from this, there is much greater variation in thyroid development than there is in brain size. The thyroid gland is affected by climate, iodine content of soil or water, season, activity of the other endocrine glands, and nervous activity. There is, however, a rough correlation between thyroid development and brain size. The relative amount of thyroid tissue in the Cetacea and the Primata is much greater than it is in the Pisces or Amphibia. Among the fishes, again, the degree of thyroidization is much greater in the cartilaginous than in the bony representatives. The reptiles show a higher degree of thyroidization than do the birds in our series. It must be remembered that these thyroidization data are derived from the actual gland weights, and histological differences which might in this instance favor the birds are not apparent. Thus if the cells are more closely packed in one group, or if there is more colloidal material stored in another, the effects of such differences would not necessarily appear in these calculations. The odd-toed and even-toed

ungulates are fairly evenly balanced in their degree of thyroidization; since both groups show many similarities, live under similar climatic conditions, and utilize the same type of food, such similarities might be expected.

In an intraclass comparison of the Primates it is an outstanding finding that the human race is on a higher thyroidization level than are the remaining primates. Apparently one of the features associated with being human is this relatively high degree of thyroid development. The relationship of thyroid activity to nervous activity has already been pointed out in connection with the description of endocrine activities of the gland. In another group, the Cetacea, which are warm-blooded mammals, the relatively large size of the thyroid gland may possibly be associated with the high metabolic rate required to maintain a warm body temperature in water, since this medium dissipates heat 27 times as fast as does air of the same temperature.

Brain and thyroid gland are closely associated either directly or indirectly with metabolism, and the mobilization of energy is closely linked to both organs. The thyroid gland maintains the metabolism at a definite level. The brain and peripheral nervous system are concerned in the maintenance of muscle tonus and regulate muscular activity which requires varying rates of oxidation in the contractile tissue.

Adrenal Gland. The adrenal gland, while concerned in energy release, does not play the constant role in its energy mobilization required of the thyroid gland (Fig. 256). A comparison of the degree of development of this organ in a large series of vertebrates fails to disclose the degree of regularity presented by the other two systems.

An examination of the graph portraying the status of this gland in our vertebrate series reveals an entirely different alignment from that which appeared with the brain and thyroid glands. The rodents occupy the highest position in this scale, while the primates are fourth, followed by the birds and the ungulates. It is difficult or impossible to evaluate the

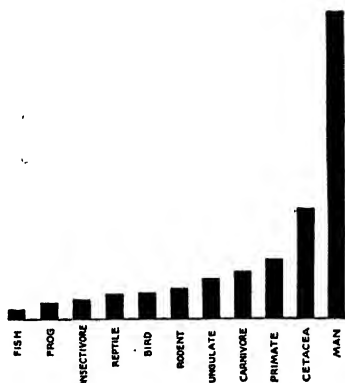


FIG. 255. The thyroidization scale.

innumerable factors that may play a determining part in the matter of adrenal size. Even though two adrenal glands might be of equal weight, there are frequently great differences in the relative amounts of medullary and cortical tissue. It may not be warranted to conclude that the erratic, shy, nervous activity of rodents is entirely due to adrenal size, although the great fluctuations in their heart rate might be explained upon this basis. The essential feature of this comparison of adrenalization is the fact that in spite of irregularities in adrenal development in various species there is an underlying approach to regularity in the different classes.

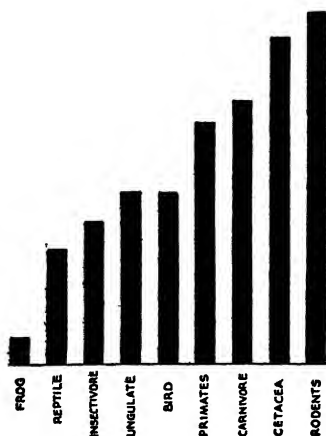


FIG. 256. The adrenal scale.

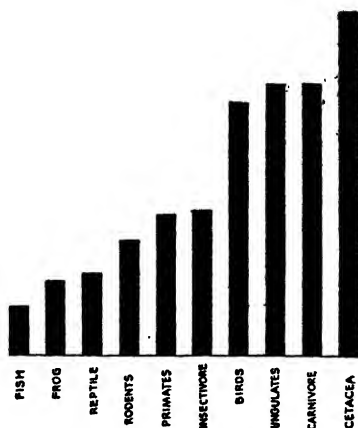


FIG. 257. The heart scale.

Heart. The size of the heart reflects the degree of activity of an animal just as its peculiar anatomical features reflect the position of the animal in the scale of being (Fig. 257). Further, its size is a measure of the blood volume in the normal animal. Hence, knowledge of relative heart size is a good criterion of the animal's habits and its rate of energy expenditure. The heart of the fish is relatively smaller than the heart of the carnivore. This inbred difference is related to difference in the vascularization of the musculature of the two orders. The hearts of three outstanding thoroughbred stallions in the Crile collection were larger than those of Percheron work horses of much greater body weight. This characteristic may have been acquired in part and in part inbred. An orderly comparison of a large series of vertebrates of various classes shows a very great advance in heart size from fish to the carnivores or

Cetacea. The hearts of birds, ungulates, and carnivores appear to have evolved to about the same levels, while the primates as a class show a lower degree of cardiac development.

Individual variations in the cephalization factors are high in the ungulates and carnivores. The two groups show some degree of parallel development in heart size, however. Among the carnivores the dog-like show higher cardiac values than do the cat-like, while in the ungulates the odd-toed show higher values than the even-toed. The domestic pig shows the lowest value among the latter; the Barren Ground caribou, the highest. In the odd-toed group the tapir and burro are at the bottom of the scale, while three thoroughbred stallions are at the top.

The graphs showing the various levels of cephalization, thyroidization, adrenalization, and heart development might indicate that the steps leading from what we term simple, or low, animals to complex, or high, animals appear planned, but we prefer an alternate explanation, namely, an explanation which implies increasing correspondence with the environment. This, of course, is an unconscious correspondence made possible through fortuitous mutations. As an example, we may cite the evolution of winged birds. Before the advent of birds, apparently none of the chordates had achieved wings, unless the fins of the flying fish are so construed. Wings were a gradual development in avian ancestry, apparently the result of repeated mutations that not only affected the wing itself but that rebuilt the covering of the skin and reshaped the body, the bones, respiratory tree, and eye. If the bird as such had been planned, we should assume a sudden appearance, omitting the countless small steps, the many failures, the occasional successes, and the final achievement—a warm-blooded, highly compact, and efficient mechanism, representing a perfect union of wing and air, capable of annihilating distance and only lately imitated by flight mechanisms built by man. We may look upon such mutations as adaptive in the sense that they fit their possessors for particular modes of life, and in the preceding pages we have emphasized the consequences of some of these adaptive modifications.

These observations do not contradict the findings of the physiologist, although the methods may be different. The physiologist of necessity must examine function, and he interferes with function within a limited field. He may reduce his variables to a very few in contrast to those operative within the normal animal or within two animals, when they are compared as we have compared them. Unless we are willing to assign differences in animal behavior to the unknown, we must, in order to arrive at some idea of the causes of these differences, examine those

systems which we know are responsible for certain specific effects in the energy-releasing mechanisms of the animals involved.

Development of Biological Thought. Comparative anatomy had its beginnings far in the past as a descriptive science. From this stage it passed gradually to the status of a science in which description became the basis of far-reaching conclusions. Lucretius', Goethe's, Erasmus Darwin's, Charles Darwin's conceptions of evolution had their origins in a measure from comparative anatomical data.

Those who came shortly after Charles Darwin, and who were in part contemporary with him, *e.g.*, Cuvier, Gegenbaur, Haeckel, Wiedersheim, the Hertwigs in Germany, Brooks, Kingsley, Parker, Cope, and Scott in this country, through their intensive studies lent plausibility to the evolutionary theory, which led to its general acceptance. While our present-day notions of the mechanism of the process are quite different from the concepts of Lucretius or Darwin, we have, nevertheless, utilized the evidence built up by patient workers since Darwin's day for our modern concepts.

Two or three generations ago biological subjects were generally taught from a static viewpoint. Even today, in some college and graduate courses, the viewpoint that degree of development of a system might be correlated with its functions is never once stressed. Under such instruction, pictures carried away from the subject, *e.g.*, classification, physiology, cytology, are isolated bits, appearing as static as the early Linnaean concept of the fixity of species. Physiology means frog gastrocnemius muscle tests, vagal stimulation and its effect on the turtle heart. Cytology is the observation of cells and includes drawing them, with copious stippling to represent cell inclusions. The dynamic nature of the cell membrane, its structure, and the electrical phenomena associated with its functions are not touched on, or if they are considered, it is in such a manner that the life of the subject is lost. The descriptive side of comparative anatomy has probably been the most satisfying subject presented, because it is so verifiable. A good manual, some experience in dissection, and the verification of the described structures in the body of the animal under dissection are a satisfying experience.

With the advance of genetics and the introduction of courses in this subject, this discipline comes nearest to satisfying at the next level, for here biology is shown to approach real exactness, and the horizon-opening experiences of reading Shull or Sinnott and Dunn and solving the problems associated with the text convert biology to a living subject.

Today comparative anatomy has widened its horizons, and although the anatomist does not wish to escape description and fact, they may be

united in such a manner that we build a series of conclusions that explain or transcend the individual details and introduce us to function. The organism is causal, and those who study it must approach it from a causal viewpoint; therefore the approach to function through the structural route appears both natural and logical.

As students of comparative anatomy we may look upon the world of animals about us as dynamic rather than as static processes. Our very concepts of species have become dynamic; species represent a process in flux, a changing stream pushing onward, guided by innumerable forces, a process compelled by its own strength and impetus into definite directions and lines, flowing into the unknown. Leaving eddies at this point, whirlpools at others, rapids alternating with quiet stretches, influencing profoundly the sphere through which it flows, the stream of living things moves onward.

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APPENDIX

BODY AND ORGAN WEIGHTS OF 3,581 VERTEBRATES

Catalogue number	Sex		Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
	Number of animals													
47F	1	M	Ray, electric, <i>Torpedo torpedo</i>	0.345	0.78	0.029	...	0.22	6.9	1.3	12.9	Key West, Fla.
1F			Ray, sting, <i>Dasypatis sebina</i>	17.58	76.52	1.76	...	47.58	815	30.67	107.2	Key West, Fla.
73F	2	M	Ray, sting, <i>Dasypatis sebina</i>	2.675	6.03	0.084	...	6.83	Key West, Fla.
9F	1	F	Shark, sand, <i>Charcharias titoralis</i>	35.38	48.8	1.81	...	41.6	2,375	44.24	96.4	...	98.82	Miami, Fla.
4F	1	M	Shark, tiger, <i>Galeocerdo tigris</i>	35.83	50.03	2.57	...	40.14	2,925	52.21	150	750
72F	1	F-P	Shark, tiger, <i>Galeocerdo tigris</i>	123	82.55	4.05	...	115	...	40.8	Miami, Fla.
74F	1	F	Shark, tiger, <i>Galeocerdo tigris</i>	200	107.5	12.73	...	291.5	40,370	88.43	Miami, Fla.

ELASMOBRANCH FISHES

BONY FISHES

63F	1	F	Barnoula, <i>Sphyracna</i> <i>barracuda</i>	4.803	1.34	0.064	7.78	38.93	25.25	260	Key West, Fla.
35F	1	M	"	5.990	3.83	0.11	12.25	62.7	29.07	409	Key West, Fla.
59F	1	F	"	8.675	2.70	0.060	11.60	80.31	45.21	430	Key West, Fla.
31F	1	M	"	9.150	6.3	60.31	38.39	Key West, Fla.
147F	1	M	"	11.33	3.93	19.27	52.54	Miami, Fla.
1480	1	F	"	12.69	4.23	0.345	16.05	44.50	160	Miami, Fla.
25F	1	M	Bonita, <i>Gymnosarda</i> <i>allesterii</i>	6.291	3.57	0.051	29.43	128	33.8	351	Key West, Fla.
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617	1	Pike, <i>Esox lucius</i>	0.82	0.597	3.9	Lake Erie, Cleve- land
1157	4	M	" "	0.3523	0.464	0.0047	0.660	3.55	4.88	1.777	0.421	Lake Erie, Cleve- land
1158												21.67	
1160													
1162	2	F	" "	0.3738	0.535	0.0118	0.560	3.780	4.915	1.555	0.420	Lake Erie, Cleve- land
1159													
1161													
1479	1	F	Sailfish, <i>Istiophorus americanus</i>	25.20	2.74	49.15	116.32	Miami, Fla.
1207													
1208	4	F	Salmon, <i>Salmo salar</i>	5.361	1.143	0.0170	10.72	96.56	8.014	39.56	11.71	Atlantic Ocean, off Maine coast
1209													
1211													
1210	2	M	" "	4.922	1.029	0.010	15.22	69.46	7.84	36.20	11.00	Atlantic Ocean, off Maine coast
1212													
965	1	M	" "	3.93	1.257	0.035	6.42	Atlantic Ocean, off Maine coast
694	1	F	" "	5.412	1.387	0.137	7.92	79.7	8.9	Atlantic Ocean, off Maine coast
1440	1	F	Shad, <i>Alosa ohienae</i>	0.615	0.527	0.010	2.21	1.91	4.25	Atlantic Ocean, off Maine coast
1441	1	F	Sheepshead, <i>Aplodi- natus grunniens</i>	0.937	0.891	0.012	1.71	6.88	Port Clinton, Ohio
620	1	Snook, <i>Omurus mor- dax</i>	0.04766	1.09	0.006	1.29	Port Clinton, Ohio
14	1	M	Snapper, vermillion, <i>Rhombopites auro- rubens</i> (Cuvier and Valenciennes)	0.202	0.65	0.006	0.33	1.76	2.54	Lake Erie, Cleve- land
1178	1	M	Trout, brown, <i>Salmo trutta</i>	0.292	0.570	0.007	0.365	3.585	2.29	1.25	1.205	Key West, Fla.
1213													
1214													
1215	5	F	Trout, northern, <i>Crie- stomer namaycush</i>	3.24	1.323	0.0134	5.17	52.43	9.33	27.97	1.77	Castalia, Ohio
1216													
1317													
													Manitowlin Island, Ont.

BONY FISHES—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
1218	1	M	Trout, northern, <i>Cristiomer, namaycush</i>	2.50	1.233	0.0095	4.34	36.00	7.26	20.92	2.16	154.7	Manitoulin Island, Ont.
1170	4	F	Trout, rainbow, <i>Salmo trident</i>	0.2177	0.415	0.0044	0.280	2.156	1.519	1.093	0.585	19.35	Adult, Castalia, Ohio
1173															
1174															
1175															
1171	2	M	" "	0.2608	0.454	0.0074	0.307	2.598	1.809	1.443	0.54	25	Adult, Castalia, Ohio
1172															
11763	1	F	" "	0.1101	0.315	0.0022	0.155	1.415	1.13	0.485	0.265	8.00	Yearlings, Castalia, Ohio
1177	1	" "	0.0428	0.178	0.0028	0.095	0.610	0.665	0.123	0.115	4.25	Infant, Castalia, Ohio
1185	2	M	Trout, salmon, <i>Salmo gairdneri</i>	2.75	0.818	0.0163	6.22	40.74	4.35	20.64	2.86	89.38	Churchill, Canada
1186	1	M	Trout, speckled, <i>Salvelinus fontinalis</i>	0.85	0.83	1.9	25.5	Pennsylvania
697	1	F	" "	0.255	0.439	0.99	5.86	2.02	0.22	16.01	Pennsylvania
696	1	M	" "	0.2301	0.466	1.15	3.75	1.94	3.32	0.17	28.24	Pennsylvania
26	1	M	Tuna, <i>Thunnus secundoides</i>	5.21	3.09	0.056	31.22	139	85.81	216	Key West, Fla.
15	1	M	Turbot, <i>Scophthalmus maximus</i>	0.295	0.872	0.005	0.364	12.86	3.36	0.09	5.54	Key West, Fla.
1145	3	M	Whitefish, <i>Coregonus clupeaformis</i>	0.7465	0.593	0.0153	0.892	8.84	2.34	7.98	0.75	42.88	Lake Erie
1149															
1180															
1146	3	F	" "	0.7886	0.593	0.0091	0.973	10.61	2.69	8.2	0.60	38.67	Lake Erie
1147															
1148	1	F	Yellowtail Ocyurus chrysurus (Bloch)	0.255	0.94	0.007	0.37	2.41	4.2	1.45	0.30	7.72	Key West, Fla.

AMPHIBIA

	1	M	Bullfrog, <i>Rana cates-</i> <i>biana</i>	0.339	0.033	0.06	1.37	6.42	2.23	1.73	1.81	North Carolina
650														
1179)														
1180)														
1181)														
1182)	6	M	" "	0.5199	0.4625	0.0336	0.1342	1.65	14.77	2.57	1.421	2.76	0.373	Louisiana
1183)														
1184)														

REPTILES

	1	M	Alligator, <i>Alligator</i> <i>mississippiensis</i>	0.105	0.35	0.40	1.39	Infant
233														
1191)	2	M	" "	0.351	1.61	0.176	0.076	1.62	6.99	1.73	1.52	2.97	0.211	Infants, Fla.
1192)	134	F	" "	3.50	4.00	161	Jacksonville, Fla.
628	1	F	" "	52.4	7.23	4.28	6.62	137	708	15.96	393	Great Lakes Ex-
														position
171	1	M	" "	80 est.	3.11	12.85	Cumberland Is-
														land, Ga.
218	1	M	" "	109 est.	8.40	6.90	5.80	92.20	1.770	Muss Island, Fla.
71F	1	M	" "	173	11.20	8.83	5.40	255	900	30.86	1.400	Miami, Fla.
1251	1	M	" "	205	14.08	13.32	11.96	318	522	25.54	628	135	Florida
183	1	F	Crocodile, <i>Crocodilus</i> <i>americanus</i> ".....	90 est.	3.77	4.17	Muss Island, Fla.
186	1	M	" "	134	15.60	5.20	4.30	134	1,145	1,125	Muss Island, Fla.
670	1	F	Gila monster, <i>Helo-</i> <i>derma suspectum</i>	0.514	0.729	0.152	0.056	4.17	35.00	6.45	Arizona
713	1	F	Iguana lizard, <i>Iguana</i> <i>iguana</i>	1.34	0.117	0.215	2.60	33.35	3.70	Guatemala, C. A.
68F	1	F	Iguana lizard, * <i>Am-</i> <i>phylachnus cristat-</i> <i>us</i>	4.19	1.44	0.040	0.090	21.51	60.40	1.06	11.60	64.4	Galapagos Islands
.....	15	M	Lizard, <i>Lacerta viridis</i> .	0.050	0.121	0.008	0.020	2.50	0.58	0.080	Europe—data from
		and F												Nacozari

* Preserved weight.

REPTILES.—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
59	1	F	Lizard.....	0.024	0.134	0.005	0.004	0.091	0.028	0.144	0.21				Maji Moto, Africa
679	1	F	Snake, black, <i>Colester constrictor</i>	0.560	0.271	0.131	0.182	6.08							Little Mountain, Ohio
1190	1	M	"	0.286	0.303	0.056	0.058	0.990	2.57	0.210	2.58	3.45	0.78	12.02	Laboratory Specimen
616	1	F	"	0.417	0.299	0.114	0.103			0.165		4.13			Little Mountain, Ohio
710	1	F	Boa, <i>Imperator</i> , <i>Boa imperator</i>	1.829	0.440	0.15	0.15	5.64	30.37	0.550	9.57	14.0			Guatemala, C. A.
668	1	F	Snake, garter, <i>Thamnophis sirtalis</i>	0.052	0.077	0.020	0.076	1.02							Willoughby, Ohio
880	1	F-P	"	0.087	0.123										Willoughby, Ohio
1139	2	M	Toad, horned, <i>Ptychocheilus cornutus</i>	0.025	0.1383	0.0044	0.0083	0.1264	0.5705	0.3927	0.6397	0.5705	0.0311		Arizona
1137	3	F	"	0.0249	0.1269	0.0070	0.0087	0.1001	0.8857	0.2761	0.2257	0.6174	0.0106		Arizona
1138	1	M	Python, <i>Python molurus</i>	6.140	1.123	1.33	2.68	19.50		1.12					Enguruka, Africa
1141	20	M and F	Snake, water, <i>Tropidonotus nativus</i>	0.070	0.1	0.01	0.035		2.80		0.88		0.12		Europe; data from Naccarati
667	1	F	Water moccasin, <i>Aplocheilichthys pictoratus</i>	0.728	0.64	0.50	1.06	4.77	64.45	0.61	13.47	22.62	5.57	300	Everglades, Fla.
	6	M and F	Snake, green water, <i>Zootoca viridiflora</i>	0.22	0.209	0.045	0.08		4.82		1.93		0.125		Europe; data from Naccarati
	20	M and F	Turtle, <i>Emys europaea</i>	0.250	0.25	0.025	0.028		7.3		1.38		0.16		Europe; data from Naccarati

	30	M and F	Turtle, <i>Testudo graeca</i> .	0.320	0.30	0.086	0.031	8.5	1.55	31.95	0.18	Europe: data from Naccarati
700	1	M	Turtle, <i>Clemmys guttata</i> .	2.163	1.36	0.125	0.413	7.05	8.45	108.5	2.25	Thompson, Ohio
68A	1	F	Turtle, <i>Chelydra serpentina</i> .	5.125	0.98	0.48	0.62	13.43	24.50	85	Maji Moto, Africa
63F	1	F	Turtle, green, <i>Chelonia mydas</i> .	88.04	5.81	3.46	3.27	180	21.08	62.57	Key West, Fla.
6F	1	M	" "	114.30	8.60	24.55	3.84	435	66.20	2,650	250	Key West, Fla.
1252	1	M	Turtle, <i>Clemmys guttata</i> .	0.185	0.57	0.20	4.40	Cleveland, Ohio
325	1	F	Turtle, leatherneck, <i>Ameyda ferox</i> .	3.253	2.50	0.51	0.44	16.0	15	Key West, Fla.
601	1	M	Turtle, snapping, <i>Macrochelys lacertina</i> .	1.848	1.01	0.59	0.51	12.88	15.9	34.90	16.41	Sandusky, Ohio

BIRDS

702	1	M	Blackbird, <i>Quiscalus quiscula oahuensis</i>	0.082	2.92	0.0116	0.0133	1.159	2.63	1.917	1.299	1.743	0.051	6.38	Little Mountain, Ohio
261	1	F	Bluebird, <i>Sialia sialis sialis</i>	0.034	1.281	0.006	0.022	0.383	Little Mountain, Ohio
262	1	M	" "	0.029	1.392	0.0093	0.013	0.493	Little Mountain, Ohio
168	1	F	Bustard, greater, <i>Choriotis kori, struthionculus</i> (Neumann) ..	5.540	12.94	0.44	0.33	60.25	98.61	40.25	22.09	70.48	490	Athi Plain, Africa
169	1	M	" "	10.00	15.63	0.91	0.87	97	200	52.45	66.42	100	655	Athi Plain, Africa
136	1	F	Bustard, lesser, <i>Halioeetus boettger boettger</i> (Daubin).....	1.100	7.62	0.213	0.237	11.93	17.63	10.18	6.07	14.35	120	Maji Moto, Africa
16A	1	M	Buzzard, steppe, <i>Buteo vulpinus vulpinus</i> (Gloger).....	0.500	7.9	0.18	0.26	4.58	10.87	3.36	4.64	Maji Moto, Africa

111)	2	M	Eagle, tawny, <i>Aquila</i>	2.438	13.91	0.31	0.50	14.17	37.55	30.96	13.57	23.18				Maji Moto, Africa
112)			razor vepoz (Temminck)													
114A	1	F	Egret, great white, <i>Casmerodius albus melanorhynchos</i> (Wagler)	1.03	6.12	0.13	0.21	9.25	33.02		8.16	33.10			135	Maji Moto, Africa
113A	1	M	Egret, yellow-bill, <i>Megascopus intermedius</i>													
109)			<i>brachyrhynchos</i>	0.525	4.7	0.07	0.14	5.0	16.53	5.16	3.72	5.35			50	Maji Moto, Africa
110)	3	F	Flamingo, <i>Phoenicopterus minor</i> (Geoffroy)	1.483	6.99	0.27	0.34	14.08	40.27	2.97	17.02	21.35			245	Maji Moto, Africa
111)				1.568	8.05	0.57	0.59	13.53	40.91	3.82	19.0	23.32				Maji Moto, Africa
116)	2	M	"													
117)																
718)																
719)	4	F	Fowl, Leghorn, <i>Gallus gallus domesticus</i>	1.263	3.916	0.2153	0.186				10.05	10.48	2.20	90.99		Cleveland, Ohio
720)																
721)	7	F	"	0.0437	0.9971	0.0038	0.0095		1.8524							6 days old
	13	M	"	0.0464	1.0556	0.0036	0.0147		1.8242							6 days old
	6	F	"	0.0682	1.2107	0.0063	0.0163		3.4452							13 days old
	14	M	"	0.0801	1.3378	0.0083	0.0185		3.1548							13 days old
	15	F	"	0.1197	1.5001	0.0094	0.0198		4.2529							20 days old
	15	M	"	0.1197	1.5411	0.0089	0.0203		4.2091							20 days old
	12	F	"	0.1719	1.7148	0.0132	0.0228		5.1676							27 days old
	8	M	"	0.1601	1.7039	0.0113	0.0254		5.0124							27 days old
	10	F	"	0.2231	1.9261	0.0167	0.0305		6.1386							35 days old
	10	M	"	0.2273	1.9173	0.0143	0.0368		6.6918							35 days old
	12	F	"	0.2951	2.1168	0.0233	0.0390		8.4172							48 days old
	8	M	"	0.3168	2.1142	0.0198	0.0441		9.0164							48 days old
	6	F	"	0.3978	2.3487	0.0300	0.0498		11.843							62 days old
	11	M	"	0.3918	2.3334	0.0294	0.0611		13.719							62 days old
	10	F	"	0.3596	2.3811	0.0269	0.0604		11.032							87 days old
	10	M	"	0.3532	2.4880	0.0336	0.1135		12.365							87 days old
	10	F	"	0.4907	2.5822	0.1097	0.0989	2.80	12.761	3.34	3.83	3.88	0.78			108 days old
	10	M	"	0.5007	2.8056	0.0631	0.1265	3.18	15.505	3.75	4.34	4.39	0.68			108 days old
	16	F	"	0.6151	2.7224	0.0762	0.0973	3.91	14.498	3.58	4.17	3.78	0.95			136 days old
	8	M	"	0.7331	2.9279	0.0894	0.0714	4.19	16.188	4.25	4.54	4.41	0.97			136 days old

BIRDS—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
602	1	M	Fowl, White Orpington, <i>Gallus gallus domesticus</i>	2.200	3.55	0.140	0.260	8.76	45.9	6.39	12.9	13.17		325	Cleveland, Ohio
18A	1	F	Goose, Egyptian, <i>Aegypen aegyptius</i>	1.935	7.64	0.34	0.42	18.51	34.31		9.75	35.2			Lake Manyara, Africa
188A	1	M	Guinea fowl, <i>NNumida meleagris</i>	1.620	4.20	0.293	0.36	14.22	28.6		7.34	29.08			Maji Moto, Africa
25	1	M	Gull, Bonaparte's, <i>Larus philadelphia</i>	0.205	2.49	0.0216	0.0329	3.44	9.12	3.14	3.20	7.12		21.56	Churchill, Canada
44F	2	F	Gull, herring, <i>Larus argentatus</i>	0.535	5.06	0.040	0.133	5.24	27.33	7.74					Key West, Fla.
10F	1	F	Gull, ring-billed, <i>Larus delawarensis</i>	0.720	8.73	0.051	0.12	7.35	23.51	8.74	7.45	9.13		154	Key West, Fla.
83F	1	F	Gull, shearwater, <i>Puffinus griseus</i>	0.268	3.01	0.031	0.049	2.46	10.03	3.27	3.23	2.45		18.21	Key West, Fla.
21F	1	F	Hawk, red-tailed, <i>Buteo borealis</i>			0.107	0.114				1.216				Little Mountain, Ohio
145	2	F	Hawk, sharp-shinned, <i>Accipiter velox velox</i> (Wilson)	1.029	10.025	0.0656	0.2035	6.94	14.10	21.22	6.87	9.27		18.38	Juvenile, W-loughby, Ohio
681	1	F	" "												Little Mountain, Ohio
229	1	F	" "	0.520	5.70	0.042	0.110	3.70				7.7			Little Mountain, Ohio
86F	1	M	Hawk, sparrow, <i>Falco sparverius sparverius</i> (Linnaeus)	0.112	2.51	0.016	0.028	1.12	2.52	3.30	1.11	1.52		7.43	Key West, Fla.
163	1	M	Hornbill, ground, <i>Buccorvus cafer</i>	3.250	26.25	0.23	0.25	56.61	57.78	35.45	23.30	52.27		290	Maji Moto, Africa
712	1	F	Hummingbird, <i>Amazilia taczanowi taczanowi</i> (De la Llave)	0.0048	0.1998	0.00045	0.00035	0.1138	0.2511	0.1201	0.0391	0.0951			Samayac, Guatemala, C. A.

55B	1	F	Loon, red-throated, <i>Gavia stellata</i>	1.580	6.12	1.33	0.223	22.72	60.87	5.47	22.71	22.62	97.42	Tavane, Canada
55A)	2	M	" "	1.568	6.38	0.210	0.219	22.24	74.02	4.89	27.61	22.31	106.27	Tavane, Canada
55C)	1	M	Man-of-war bird, <i>Fregata aquila</i>	1.405	9.45	0.089	0.175	16.59	35.88	12.99				Key West, Fla.
52F	1	F	Merganser, red-breasted, <i>Mergus serrator</i>	0.770	5.289	0.0657	0.1033	11.01	19.77	2.76	9.67	18.16	46.30	Tavane, Canada
90A	1	M	Ostrich, Massi, <i>Struthio camelus massaius</i> (Neumann).....	123	42.11	17.33	23.01	1,205	2,050	95.26	920	2,900	23,133	Maji Moto, Africa Zoo specimen, Cleveland, Ohio
143	1	M	" "			5.5								
225	1	M	Owl, horned, <i>Bubo virginianus virginianus</i>	1.177	13.70	0.085	0.165	8.60				10.7		Little Mountain, Ohio
6A	1	M	Partridge, Francolinus <i>sephanus</i>	0.208	1.50	0.02	0.033	1.46	8.65		2.70			Maji Moto, Africa
7F)	2	F	Pelican, <i>Pelecanus occidentalis</i>	3.280	17.95	0.183	0.993	22.12	73.15	12.73		29.83	255	Key West, Fla.
23F)	1	M	Pheasant, <i>Phasianus colchicus</i>	0.625	3.289	0.051	0.12	5.61	9.115	5.32	4.82		56.5	Little Mountain, Ohio
1257														
263	1	M	Phoebe, <i>Sayornis phoebe</i>	0.0181	0.793	0.006	0.005		0.207					Little Mountain, Ohio
264	1	F	" "	0.0175	0.750	0.0025	0.0055	0.165						Little Mountain, Ohio
271	1	F	Pigeon, <i>Columba livia</i>	0.247	2.285	0.031	0.046	4.651				4.09		Little Mountain, Ohio
268)	3	M	" "	0.262	2.664	0.028	0.0421	4.836				5.07		Little Mountain, Ohio
269)														
270)														
24A)	3	M	Parnigan, willow, <i>Lepopus lasopus</i>	0.542	2.377	0.0255	0.0273	7.863	12.99	2.316	3.87	9.61		Churchill, Canada
24C)														
24D)	1	F	" "	0.540	2.800	0.017	0.036	9.46	13.405	3.022	4.870	10.74		Churchill, Canada

BIRDS.—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
108	1	F	Raven, <i>Corvus corax</i>	0.031	2.428	Catalina Mountains, Arizona
288 289	2	M	Robin, <i>Turdus migratorius migratorius</i>	0.0603	2.09	0.0105	0.0213	1.018	1.077	Little Mountain, Ohio
28	1	F	Scaup, greater, <i>Nyroca morila</i>	0.787	4.7859	0.0855	0.1850	8.00	23.00	1.76	9.11	18.01	99.15	Churchill, Canada
	11	F	Sparrow, <i>Passer domesticus</i>	0.02326	1.0185	0.0041	0.0069	0.3028	1.0873	0.5179	0.357	0.3996	0.0428	2.081	Cleveland, Ohio
	75	M	" " " " " " " "	0.02357	1.0278	0.0042	0.0063	0.4077	1.2062	0.4591	0.345	0.3074	0.0426	2.098	Cleveland, Ohio
285	1	F	Sparrow, song, <i>Melospiza melodia</i>	0.021	1.10	0.0145	0.005	0.235	Cleveland, Ohio
14A	1	M	Stork, Abdim, <i>Sphenorhynchus oblitus</i> (Lichtenstein).....	0.950	7.3	0.23	0.46	8.40	27.94	8.88	8.80	10.36	Maji Moto, Africa
84A	1	M	Stork, European, <i>Ciconia ciconia ciconia</i> (Linnaeus).....	3.350	16.24	0.43	0.49	28.75	71.4	18.30	26.24	27.2	Maji Moto, Africa
83A 83A	2	F	" " " " " " " "	3.350	15.78	0.40	0.44	32.12	61.06	16.5	19.84	42.26	Maji Moto, Africa
106A	1	M	Stork, hammerhead, <i>Scoptes umbretta</i>	0.3175	3.93	0.037	0.061	7.22	8.16	Maji Moto, Africa
107A 108A	2	M	Stork, Marabou, <i>Leptoptilos crumeniferus</i> (Lesson).....	7.130	30.14	0.64	2.06	55.24	110	27.89	42.94	72.23	602	Maji Moto, Africa
287	1	M	Swallow, barn, <i>Hirundo erythrogastra</i>	0.0215	0.904	0.006	0.007	0.302	Little Mountain, Ohio
288 289	2	F	" " " " " " " "	0.021	0.879	0.0083	0.0085	0.283	Little Mountain, Ohio
27	1	F	Teal, green-winged, <i>Nettion carolinensis</i> .	0.305	3.116	0.0281	0.0430	2.88	8.17	1.16	3.105	9.218	42.0	33.94	Churchill, Canada

CETACEA

70	1	M	Porpoise, <i>Phocaena phocaena</i>	142.43	1,735	18.29	10.41	738	2,962	57.19	5,250	53.02	13,255	Key West, Fla.
1	2	F	Whale, white, <i>Delphinapterus leucas</i>	303.23	2,354	65.94	29.23	1,722	4,825	22.01	1,857	7,936	153	9,296	Churchill, Canada
32	7		"												
19	4	M	"	447.03	2,349	111.04	29.20	2,454	6,807	31.71	2,214	12,093	200	12,075	Churchill, Canada
33			Whale, blue, <i>Balaenoptera musculus</i>	58,059	6,800	3,450	1,335								Queen Charlotte Islands, Canada
34	1														
748			Whale, finback, <i>Balaenoptera physalus</i>	59,394 (130,946 lb.)											Whaling Station, Fields Landing, Calif.
5C	1	F	Whale, humpback, <i>Megaptera nodosa</i>	37,165 (82,000 lb.)	5,238 (11.66 lb.)	3,237 (7.13 lb.)		214,000 (472 lb.)	478,000 (1,050 lb.)		192,000 (424 lb.)		6,045 (13.33 lb.)		Whaling Station, Fields Landing, Calif.
4C	1	M	"	39,916 (88,000 lb.)	6,800 (15 lb.)			181,000 (400 lb.)	363,000 (800 lb.)						Whaling Station, Fields Landing, Calif.
1C	1	M	"	40,823 (90,000 lb.)	7,229 (15.94 lb.)	2,960 (6.52 lb.)	1,210 (2.66 lb.)	193,000 (425 lb.)	635,000 (1,400 lb.)	980 (2.16 lb.)					Whaling Station, Fields Landing, Calif.
2C	1	M	"												
3C	1	M	Whale, sperm, <i>Physeter catodon</i>	39,009 (86,000 lb.)	4,023 (8.88 lb.)	800 (1.76 lb.)	350 (0.077 lb.)	126,000 (277 lb.)	420,000 (925 lb.)	290 (0.64 lb.)					Whaling Station, Fields Landing, Calif.

CARNIVORES

133	1	M	Bear, American, <i>Euarctos americanus</i>	551.25	25.0	6.0	176.5	Zoo specimen, Detroit, Mich. (goiter)
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CARNIVORES.—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
600	1	F	Bear, grizzly, <i>Ursus horribilis</i>	142.88	233.9	53.6	65.5	1,132.5	547.8	..	304	Zoo specimen, Cleveland, Ohio
624	1	M	Bear, polar, <i>Thalarchos maritimus</i>	199.57	489	17.3	10.8	1,161	4,539	10.1	1,292	1,701	245	Zoo specimen, Cleveland, Ohio (goiter)
567	1	F	" "	317.50	507	21.5	29.8	1,220	4,126	..	730	2,580	..	Zoo specimen, Cleveland, Ohio
103	1	F	Cat, civet, <i>Spilogale arizonae arizonae</i>	6.0	0.023	0.085	3.78	Catalina Mountains, Ariz.
99	1	M	" "	0.007	0.072	4.35	Catalina Mountains, Ariz.
759	1	..	Cat, domestic, <i>Felis domestica</i>	0.576	16.0	..	0.5	3.0	31	..	7.5	7.5	2.5	Juvenile, Panama
48F	2	M and F	" "	1.542	18.0	..	1	10	86	..	16.5	15	6.5	Adult, Panama
232	2	F	" "	2.885	23.46	0.21	0.639	12.38	92.67	10.06	22.07	32.6	6.48	Key West, Fla.
1253	5	M	" "	3.778	28.37	0.408	0.571	16.82	126.8	9.67	44.5	42.7	11.7	Cleveland, Ohio
1254	5	M	" "
632	" "	5.025	28.23	0.460	0.795	19.61	184.2	11.86	49.94	28.47	11.02	Key West, Fla.
749	..	M	" (feralised)
36F	..	M	Cat, genet, <i>Genetta tigrina szechica</i> (Matschie)	1.302	15.89	0.29	0.49	7.51	49.63	3.72	8.93	12.99	..	Maji Moto, Africa
10A	2	M	" "	1.525	15.35	0.04	0.19	8.46	58.54	344	14.05	22.55	..	Maji Moto, Africa
67A	1	F	" "
104	2	M	Cat, ring-tailed, <i>Basileiscus astutus</i>	17.1	0.088	0.353	10.22	Arizona

182A	1	F	Cat, wildcat, <i>Felis oncat</i>	2,700	28.48	0.10	0.19	5.86	32.75	6.41	10.07	9.0	78	Maji Moto, Africa
148	1	M	Cheetah, <i>Acinonyx jubatus</i>	22.20	2.449	1.09				82.5			...	Zoo specimen, Cleveland, Ohio
1292	1	M	" "	40.82		13.05	2.91	189	1,000	49	145	360	47.2	Zoo specimen, Cleveland, Ohio (gotter)
	1		Coati, <i>Nasua narica panamensis</i> (Allen).		23.3		0.4	2.0	17.5		4.0	5.3	1.8	Adult, Panama
714	1	M	" "	0.399	44.17	1.54	0.54	37.97	150	2.33		43	5.50	Guatemala, C.A.
667	1	F	Coyote <i>Canis latrans</i>	8.510	84.24	0.6901	1.049	72.71	292.5	11.11	80.07	61.28	14.21	Cedar Vale, Kans.
89	1	F	" "		80.0	1.8	0.560				80.69			Kaibab Forest, Ariz. (gotter)
213A	3	M	Dog, <i>Canis familiaris</i>	14.56	79.99	1.14	1.74	127	760	10.97	84.8	362	1,553	Maji Moto, Africa
216A														—African mongrel
180A	2	F	" "	12.47	81.14	1.35	1.45	120	665	13.11	88	238	1,430	Maji Moto, Africa
212A	1	M	Greyhound.....	24.49	105.9	2.34	3.36	308.8	1,067	12.36	105.9	363.5	175	Memphis, Tenn.
36	2	M	Huskies.....	31.75	130.7	2.85	3.16	297	1,438	10.88	248	431	1,944	Churchill, Canada
57	1	M	" "	26.94	79.3	11.3	10.6				216.2			Zoo—originally from Alaska (gotter)
8F	2	F	Mongrel.....	14.75	66.53	1.11	1.09	95.4	300	9.73	44.65	108.1	712	Key West, Fla.
228F	2	M	" "	11.26	87.6	3.36	1.54	126.3	465.2	16.85		138.4		Cleveland, Ohio
362	4	F	Dog, collie-police.....	23.71	84.63	2.93	2.07	182.6	663		132	192.7		Cleveland, Ohio
369	1		" "		90	8.6	7.0							Adult, Panama
370	1	M	Dog, police.....	19.28	95.2	23.8	6.1	261						Cleveland (gotter)
367	1	F	Fox bat-eared, <i>Otocyon megalotis</i>	3.335	26.09	0.49	0.49	24.65	125	4.65	31.91	35.05	660	Maji Moto, Africa

CARNIVORES.—(Continued)

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
90	F	Fox, gray, <i>Urocyon cinereoargenteus scottii</i>	32	0.066	0.281	17.75
91	M	"	3.750	37.28	0.154	0.390	21.97	50.80	4.02	17.43	19.12	White Tank Mountains, Ariz. 425
92	M	"	38	0.266	0.329	24.09
95	M	"	White Tank Mountains, Ariz.
100	F	Fox, red, <i>Vulpes fulva</i> (Desmarest)	0.405	0.420	24.95
115	F	"	0.1469	0.5235	41.75	4.18	Little Mountain, Ohio
647	F	"	4.625	53.30	0.763	0.353	Churchill, Canada
648	M	Fox, white, <i>Vulpes lagopus inuitus</i> (Merriam)	3.385	44.50	0.763	0.353	5.8	Churchill, Canada
133A	2	Hyena, spotted, <i>Crocuta crocuta</i>	62.37	175	6.68	15.03	447	3,194	40.42	400	6,809
28A	2	Jakal, <i>Thos macrotis</i>	2.85	46	0.78	0.508	21.33	122.5	6.8	23.03	30.08
95A	M	"
140	M	"
678	F	Jaguar, <i>Felis onca</i>	34.47	147	1.72	7.46	186	894	17.28	164.5	576	62.12
709	F	Kinkajou, <i>Potos flavus astutus</i>	2.62	31.05	0.56	0.19	14.3	98.6	1.9	78.5
608	M	Leopard, <i>Felis pardus</i>	48	135	48.55	6.93	200	900	31.4	500	104.3
551	F	Leopard, infant	8.618	121	1.3	2.3	52	278	86	183

Guatemala City, Guatemala
Zoo, Detroit, Mich.
(goiter)
Zoo, Cleveland, Ohio

131	1	F	Lion, <i>Felis leo</i>	83.91 est.		23.5	14.5	455			535			Zoo, Detroit, Mich. (goiter)
135	1	F	"	90.72 est.		9.17	5.75	327.3						Beatty circus (killed in combat)
144	1	F	" (cub)	62.7 est.		7.41	7.24				325.4			Hearst Lion Farm, San Simon, Calif.
207	1	F	" (cub)	50.9 est.	166.7	165	8.4	363.5	1,360		1,200			Zoo, Toledo, Ohio (goiter)
1320	1	F	"	117.93	232	840	14 est.	810	3,825	52.40	624	2,425	265	Zoo, Cleveland, Ohio (goiter)
219	1	M	"	161.52	245.7	1,412	24.9	1,614			2,600			Zoo, Philadelphia, Penna. (goiter)
579	1	M	"	117.57	194.2	404.5	10.7	713						Zoo, Cleveland, Ohio (goiter)
689	1	M	"	94.86	247.82	95.37	21.34	743.2	2,095	51.8	477.6	1,580	157	Zoo, Cleveland, Ohio (goiter)
1450	1	M	"	126.08	248.5	1,265	14.72	1,078	3,510	55.14	684	3,838		Zoo, Cleveland, Ohio (goiter)
37A	1	M	"	195.4	261	22.52	34.64	1,175	6,000	54.72	1,610	2,000	825	Maji Moto, Africa
38A	1	M	"	186.36	255	18.62	30.82	860	5,450	63.74		2,600	265	Maji Moto, Africa
612	1	M	Lion, mountain, <i>Felis oregonensis</i> ...	28.79	106.7	2.20	9.6	184	1,255	9.2	131.7	326		New Mexico Catalina Mountains, Ariz.
106	1	F	"			1.6	4.1							Florence, Ariz.
98	1	M	<i>Lynx lynx baileyi</i> ...			0.35	0.60				24.6			
160A	1	M	Mongoose, <i>Ichneumia albicauda</i> ...	4.40	28.30	0.21	0.61	28.30	61	4.0	34.96	58		Maji Moto, Africa
571	1	M	Puma, <i>Felis bairdi</i> ...											
			<i>costaricensis</i> , (Merriam)	26.25	129	1.40	10.2							Juvenile, Panama
	1		Raccoon, <i>Procyon lotor pumilus</i> (Miller)	5.175	40	1.33	3.22							Adult, Panama
64	1	F	"	2,226	33.55	0.190	1.55	19.73	140	3.32	35.85	19.41	225	Key West, Fla.
563	1	F	"	4,536	40.5	195	1.4	31.2	136		37	38	13.8	Zoo, Cleveland, Ohio (goiter)
563	1	M	"	4,216	42.7	261	0.9	42.5	187		35.7	187	14.6	Zoo, Cleveland, Ohio (goiter)

CARNIVORES.—(Continued)

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
103F	F	Raccoon, <i>Procyon lotor puratus</i> (Miller)	0.222	1.651	Cumberland Island, Ga.
321	M	Skunk, <i>Mephitis mephitis</i>	1.700	10.3	0.274	0.468	9.82	45.7	...	10.1	27.1	New York State
110/127	F	" "	2.260	10	0.055	0.305	7.86	Cleveland, Ohio
102/111	M	Skunk, hog-nosed, <i>Conopatus mesoleucus</i>	...	15.5	0.068	0.279	11.21	Catalina Mountains, Ariz.
117	F	" "	...	16.0	0.054	0.211	7.51	Arizona
139	M	Serval, <i>Felis capensis</i>	9.955	66.74	0.42	1.03	37.3	225	18.02	100	125	...	400	Maji Moto, Africa
87/151	F	" "	5.819	53.16	0.33	0.40	28.45	86.18	10.23	40.34	50.72	...	350	Maji Moto, Africa
268	F	Tiger, <i>Felis tigris</i>	160	225	68.2	16	432	1,818	1,020	915	...	Zoo, Cleveland, Ohio (goiter)
216	M	" "	209	302	50.5	20.8	698	1,888	Jungle-bred captive
53A/53B/53C	M	Wiesel, arctic, <i>Mustela arctica</i>	0.1693	5.64	0.108	0.015	2.83	9.67	0.153	1.80	3.85	0.713	...	Tavane, Canada
762	F	" "	0.121	3.47	0.015	0.030	1.95	5.5	0.110	1.81	3.60	Cleveland, Ohio
637	M	Wolf, Russian, <i>Canis lupus lupus</i>	22.68	119	13	2.4	246	626	18.20	187	807	Zoo, Cleveland, Ohio (goiter)
672	M	Wolf, timber, <i>Canis lupinus</i>	29.94	152	3.49	3.37	315	925	16.64	223	379	44.3	...	Ely, Minn.

PINNIPEDIA

40	F	Seal, bearded, <i>Erigonathus barbatus</i>	109.7	...	6.13	6.95	515	Chesterfield Inlet, Canada, juvenile
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39	1	F	"	281	460	22.83	22.04	1,245	5,454	63.06	1,320	4,536	26,330	Chesterfield Inlet, Canada
613	1	M	Seal, <i>Phoca richardi</i>	107.3	442	10.02	6.27	1,435	4,485	60.72	894	1,880	520	California Zoo, Cleveland, Ohio
149	1	M	"	378	5.2	6.0	418
18	31	M	Seal, ringed, <i>Phoca hispida</i>	39.76	251	3.49	2.49	281	1,244	73.34	273	738	110	Churchill (2), Chesterfield Inlet (1), Canada
36	2	F	"	39.68	255	3.44	3.41	302	930	70.20	236	730	150	Chesterfield Inlet, Canada
45	1	M	Walrus, <i>Odobenus rosmarus</i> (Linnaeus).	79.38	766	17.52	8.61	731	3,625	827	520	Churchill, Canada, 3 months old
38	1	F	"	55.79	737	13.68	7.20	650	2,300	13.2	725	1,625	200	Chesterfield Inlet Canada, 3 months old
43	1	M	"	667	1,126	70.04	27.07	4,536	19,504	26.63	4,536	9,072	Tavane, Canada
46	3	M	"	595.6	66.67	20.15	Walrus Islands, off Tavane, Canada

RODENTS

1	Agouti, brown, <i>Dasyprocta punctata darwensis</i> (Goldman).....	1,400	15.00	0.5	10	60	14	10	5	Infant, Panama
3	M and F	"	2,059	12	0.48	9.2	63.22	10.7	12.89	5.23	Juvenile, Panama
2	M and F	"	3,172	18.34	0.98	17.54	85	15.39	16.0	6.04	Adult, Panama
1	M	Agouti, spotted, <i>Cuniculus paca virgatus</i> (Bangs)	0.891	20.5	0.101	0.40	Juvenile, Panama
2	M and F	"	1,373	10	1.4	5.5	65.0	10.5	16.5	5.00	Juvenile, Panama

RODENTS.—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
	3	M and F	<i>Agouti, spotted, Cuniculus paca virgatus</i> (Bangs)	3.627	21.85	1.6	16.10	187	22.7	23.5	12.07	...	Adult, Panama
1286	1	M	"	4.569	48	0.82	3.1	Adult, Panama
1290	1	F	Beaver, <i>Castor canadensis</i>	4.18	25.48	0.207	0.228	16.57	99.82	35.86	63.47	Michigan
	2	M and F	"	5.83	29.52	0.644	0.752	27.0	203	1.50	72.60	33.3	4.75	Michigan
	1	<i>Capybara, Hydrochoerus isthmicus</i> (Goldman)	27.670	52.21	5.2	84.13	577	69.75	227	50.58	Adult, Panama
33	3	M	"	7.089	24.18	113	28.06	38.50	16.3	Infant, Panama
49	2	F	<i>Capybara, Tamias striatus fisheri</i> (Howell)	14.96	2.72	55.06	5.09	81.0	88.99	75.3	Juvenile, Panama
	1.60	0.0021	0.0137	0.503	San Francisco Crater and Schultz Pass, Ariz.
703	2	M	"	0.075	2.22	0.030	0.070	0.597	5.55	0.556	0.756	0.719	0.222	4.65	Cleveland, Ohio
671
34	4	M	"	2.00	0.002	0.015	0.535	San Francisco Crater and Schultz Pass, Ariz.
35
38
51
52
55
57	5	F	Gopher, pocket, <i>Thomomys fulvus fulvus</i> (Woodhouse)	1.32	0.0041	0.012	1.15	Schultz Pass, Ariz.
41
44
53
59	2	M	"	1.35	0.0045	0.013	0.983	Schultz Pass, Ariz.

174}	2	F	Gopher pocket, <i>Geomys cumberlandius</i>				0.013	0.021									Cumberland Is-land, Ga.
175}	1	M	" "				0.016	0.006									Cumberland Is-land, Ga. (hy-perplastic thy-roid gland)
176}	1	M	" "				0.028	0.004									Cumberland Is-land, Ga.
177}	1	F-P	Guinea pig, <i>Cavia culter</i>	3.63	0.351	0.070	0.375	1.72	10.94	0.88	2.79	5.86	0.52				Young adult, Cleveland, Ohio
178}	2	M	" "	4.10	0.361	0.053	0.334	1.27	13.80	0.93	3.43	4.62	0.71				Young adult, Cleveland, Ohio
179}	2	F	" "	3.80	0.324	0.056	0.316	1.31	31.93	0.95	3.81	3.27	1.08				Young adult, Cleveland, Ohio
180}	56	F	" "	3.32	0.21494	0.036	0.180	1.29	12.06		2.829	2.934					Cleveland, Ohio
181}	46	M	" "	3.28	0.21457	0.035	0.185	1.291	11.73		2.821	2.563					Cleveland, Ohio
182}	10	F	" "	4.00	0.432	0.071	0.343	1.67	16.7	1.04	3.72	4.03	0.925				Cleveland, Ohio
183}	10	M	" "	4.23	0.456	0.096	0.402	1.86	21.17	0.84	4.16	5.12	0.760				Cleveland, Ohio
184}	2	F	Golden hamsters, <i>Cricetus cricetus</i>	128.7 gm.	1.062	0.0074	0.0118	0.600	6.76	0.226	1.27	0.583					Cleveland, Ohio
185}	2	M	" "	107.5 gm.	1.012	0.0088	0.0302	0.543	5.43	0.212	0.998	0.510					Cleveland, Ohio
186}	135	F	Hare, African, <i>Lepus capensis</i>	2.93	10.23	0.190	0.50	30.0	51.91	7.37	12.20	17.91	295				Maji Moto, Africa
187}	248	2	Hare, arctic, <i>Lepus arcticus</i>	1.901	14.36	0.180	0.240	28.45	66.11	4.59	19.29	43.79					Tavane, Canada
188}	251	2	" "	2.640	13.90	0.099	0.191	28.87	65.22	4.75	25.44	44.04					Tavane, Canada
189}	200	2															
190}	50A																
191}	50C	4	Lemming, brown, <i>Lemmus trimacrotatus</i> (Richardson).														
192}	50D			0.0292	1.126	0.0058	0.0167	0.434	2.33	0.0230	44.04	0.804					Churchill, Canada
193}	50E	1	" "	0.048	1.312	0.0046	0.0251	0.600	3.80	0.0242	0.525	0.740					Churchill, Canada

RODENTS.—(Continued)

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
3														
4	M	Lemming, rock, <i>Dicrostonyx rubricatus</i>	0.0521	0.8983	0.0042	0.0138	0.311	2.63	0.1451	0.774	0.827	0.210		Churchill, Canada
10B														
10E														
10A														
10C	F-P	"	0.0552	0.8447	0.0089	0.0177	0.381	3.05	0.062	0.841	0.884			Churchill, Canada
10D														
171	M	Mouse, African, <i>Mastomys coucha microdon</i>	0.0218	0.7132	0.001	0.0095	0.122	0.944	0.075	0.265	0.2408		2.63	Maji Moto, Africa
674														
630B	F	Mouse, jumping, <i>Zapus hudsonicus</i>	0.0193	0.6961	0.001	0.008	0.1557	1.124	0.028	0.218	0.246	0.0261		Little Mountain, Ohio
630C														
630A	M	"	0.0152	0.522	0.003	0.005	0.133	0.743	0.025	0.266	0.243			Little Mountain, Ohio
1A	F-P	Mouse, dormouse, <i>Clariglis saturatus</i> (Dollman)	0.0223	0.705	0.004	0.002	0.1132	0.851	0.063	0.192	0.205			Maji Moto, Africa
145	M	"	0.0177	0.551	0.006	0.0042	0.116	0.308	0.052	0.091	0.272		0.75	Maji Moto, Africa
66	M	Mouse, grasshopper, <i>Onychomys</i>			0.0011	0.0237				0.374				Seligman, Ariz.
68	F	"			0.0014	0.040				0.392				Seligman, Ariz.
69	M	Mouse, meadow, <i>Microtus drummondii</i>	0.237	0.6606	0.0032	0.0095	0.1612	1.082	0.0239	0.3634	0.4036			Churchill, Canada
42	F	"	0.0229	0.6464	0.0031	0.0160	0.1609	1.129	0.0236	0.3814	0.3930			Churchill, Canada
4	F-P	"	0.0325	0.6724	0.0037	0.0366	0.1999	1.754	0.0276	0.5357	0.5575			Churchill, Canada
42	F	Mouse, meadow, <i>Microtus pennsylvanicus pennsylvanicus</i>												
53	M	"	0.0252	0.7166	0.0046	0.0164	0.1973	1.349	0.0269	0.3103	0.3916			Willoughby, Ohio
10	F-P	"	0.0279	0.7394	0.0042	0.0071	0.1937	1.312	0.0254	0.3126	0.3984			Willoughby, Ohio
		"	0.0413	0.7635	0.0065	0.0305	0.2574	2.250	0.0277	0.4821	0.4999			Cleveland, Ohio

71	3	F	Mouse, mountain meadow, <i>Microtus alticola alticola</i>			0.0018	0.0068				0.233	Agassiz Peak, Ariz.
111	1	M	" "			0.0032	0.0126				0.476	Agassiz Peak, Ariz.
12	14	M	Mouse, Guatemala, * <i>Peromyscus</i>	0.0122	0.407	0.0014	0.0037	0.65	0.235	0.1477	0.22	Totonacapan, Guatemala
13	2	F	" "	0.0184	0.4511	0.0021	0.0049	0.1132	1.243	0.033	0.2157	Totonacapan, Guatemala
	8	F-P	" "	0.0200	0.443	0.0024	0.0064	0.1499	1.186	0.0291	0.2255	Totonacapan, Guatemala
	9	M	Muskrat, <i>Ondatra zibethica alba</i>	0.900	5.33	0.0133	0.143	3.23	21.95	1.83	7.45	Churchill, Canada
	1A	F	Porcupine, <i>Erethizon dorsatus</i>	2.800	30.77	0.72	0.62	19.75	112	2.8	26.97	Maji Moto, Africa
	234	2	" "	2.725	21.71	0.361	0.337	14.4	29.88	Animal dealer, New York
	389	2	" "	3.410	19.15	0.341	0.355	15.5	108	38	Animal dealer, New York
	324	1	" "								27.1	
	81	F	Prairie dog, <i>Cynomys gunnisoni gunnisoni</i> (Hollister).....			0.034	0.019				2.72	Seligman, Ariz. (in hibernation)
	84	1	" "			0.025	0.028				2.564	Seligman, Ariz.
	93	2	Rabbits, cottontail, <i>Sylvilagus auduboni</i>		5.60	0.047	0.115				6.123	Florence, Ariz.
	94	F	" "			0.031	0.094				5.14	Catalina Mountains, Ariz.
	97	2	" "		7.25							
	105	M	Rabbits, Flemish giant, <i>Lepus californicus</i>	3.680	10.59	0.685	0.503	10.57	97.9		22.35	Cleveland, Ohio
	203	22	" "	2.587	10.14	0.403	0.662	9.23	82.63		18.3	Cleveland, Ohio
	80	1	Rabbit, jack, <i>Lepus californicus</i>								13.72	
		F	Rabbits, wild, <i>Silvagus californicus</i>	12.00		0.147	0.256				19.34	Seligman, Ariz.
		2	Rabbits, wild, <i>Silvagus californicus</i> (Goldman).....	0.439	4.50		0.750	2.00	19.50		3.50	Adult, Panama

Preserved weights.

23A	4	M	"	0.183	4.71	0.023	0.049	1.57	3.99	0.497	1.14	2.66	Churchill, Canada
23B			"										
23D	1	M	"	0.169	4.45	0.068	0.142	2.132	10.79	0.806	1.930	4.016	0.511	9.79
23E			"										Little Mountain, Ohio
633E	1	M	"	0.169	4.21	0.031	0.098	1.23	5.88	0.661	1.51	1.34	Cleveland, Ohio
633F	2	F	Squirrel, red, <i>Sciurus hudsonicus</i>										
633D			"										
633A	1	M	"	0.183	3.97	0.006	0.062	1.511	4.18	0.390	1.425	3.25	Cleveland, Ohio
633C	1	M	"	0.063	4.09	0.0056	0.025	0.545	1.74	0.436	0.615	1.54	Juvenile, Cleveland, Ohio
17													
19													
23	7	F	Squirrel, red, <i>Sciurus fremontii</i>										San Francisco Crater and Schultz Pass, Ariz.
26			"										
31			"										
32			"										
60			"										
20													
21													
25													
27	7	M	"										San Francisco Crater and Schultz Pass, Ariz.
28													
29													
61													

UNGULATES

677	1	M	Bison, American, <i>Bison bison</i>	54.88	334	5.47	6.64	361	695	42.68	256	1,190	146	Calif., Zoo, Cleveland, Ohio
70A	2	M	Buffalo, <i>Syncerus cafer</i>	750 est.	640 est.	34.96	31.05	Maji Moto, Africa
80A	1	F-P	"	572	642	37.30	43.27	3,050	6,175	69.94	1,625	5,150	2,340	146,000	Maji Moto, Africa
71A	1	M	"	769	560	38.05	50.4	3,628	7,712	55.00	1,825	8,110	150,000	Maji Moto, Africa
414	1	F	Bushbuck, <i>Tragelaphus scriptus masaiensis</i>	35.38	140	6.76	4.43	325	625	40.53	131	315	92.75	Maji Moto, Africa

UNGULATES.—(Continued)

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
94A	M	Bushbuck, <i>Tragelaphus scriptus masaisius</i>	53.07	190	5.08	5.09	350	1,100	...	225	540	...	6,700
1481	M	Camel, <i>Camelus bactrianus</i>	453.59	569.5	165.5	25.5	99.0	387	...
852	F	Caribou, Barren ground, <i>Rangifer arcticus arcticus</i>	71.87	278	3.99	2.29	710	466	33.35	82.77	1,275	131	...
44 (853)	M	" "	128.47	306	8.37	5.99	1,086	2,445	41.66	151	2,450	310	25,400
42	M	" "	62.14	285	5.98	4.16	650
1428	F	Cow,	408.23	363.8	18.8	25.0	...	3,959	52.8	834.0
1432	F	" "	378.75	491.5	39.6	13.0	2,018	3,637	75.5	726.0	5,784
1*	F	Aberdeen Angus,	719	...	57.5	57.50	1,950	6,690	...	1,746	2,654	839	21,682
44*	F	Ayrshires,	491	417.3	33.4	31.2	1,882	6,010	...	1,148	3,311	817	25,156
5	F	Cows,	11.82	18.07
6	F	" "	21.03	24.01
62*	F	Guernseys,	430	403.1	31.6	27.7	1,737	6,087	...	978	3,143	832	23,523
7*	F	Hersfords,	371	357	15.24	18.46	1,143	3,819	...	672	2,272	561	20,734
20*	F	Holsteins,	574	414	38.1	37.7	2,245	7,243	...	1,445	4,336	946	29,184
8*	M	Holstein bulls,	90	259	14.25	6.37	422
3*	M	" "	241	386	30.2	10.13	998
5*	M	" "	552	467.7	41.4	19.76	1,905
2*	M	" "	861	471	45.5	22.5	3,243
5*	M	" "	868	432	95.34	41.6	3,357
218*	F	Jerseys,	413	408	27.9	27.4	1,605	5,747	...	983	3,057	801	22,230
3*	F	Jersey bulls,	51.9	304	6.4	5.35	304

	6-12 months old	1-3 years old	3-5 years old	Over 5 years old	Average 8 years 2 months old	Cleveland, Ohio
5* M	214	356	19.38	9.73	744	812
2* M	367	394	20.05	14.5	1,270	
2* M	591	444	47.00	18.3	1,987	
10* M	597	447	82.20	27.45	2,186	
213* M	412	408	27.90	27.40	1,606	
71* F	506	420	35.2	303.3	1,888	1,207
6 M			18.8	20.68		3,978
15 M	174		13.9	16.57		
18* M	369	384	20.87	13.16	1,533	423
1380		203.6	4.7	5.2	234.5	505.2
1 M			8.3	5.4		32.6
1 M	10.80	143.1			433	22.5
1 M	19.5	193.9	8.0	29.4	220.5	29.4
1 F	98.43	387.5	12.1	9.4	810.7	2,938
1386	23.36	187.9	6.9	4.8	174.2	535.8
1 M	22.0	215.2	19	32.5	265.3	1,008.8
1387		234.6	12.6	3.0	315.3	792.3
1 F	489.9	473.5	46.1	17.4	2,601	6,265
2	2,376	54.1	0.2	0.62	5.16	72
1 F	13.93			3.0	15.9	516
1 M			20	8.6		280
1 M	88.45	219	17.5	6.45	749	1,730
1 M	148		25	30.6		317
184			2.33	2.83		
181						
182						

* Data from *Journal of Agricultural Research*, Vol. 55, No. 4, Aug. 15, 1937. W. W. Swett and Associates.

UNGULATES.—(Continued)

Catalogue number	Number of specimens	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	Locality
172	2	F	" "			2.12	2.30								Cumberland Is-land, Ga.
177	1	M	" "	65.22	210	5.1	12.25	632	1,025			1,318			Zoo, Detroit, Mich
272	1	M	Deer, white-tailed, <i>Odocoileus couesii</i>		172	2.50	3.25				115				Kaibab Forest, Ariz. (goiter)
112	2	M	" "		122	1.65	2.49				85				Kaibab Forest, Ariz.
114	1	F	" "												
101	1	F	" "												
86	3	M	Deer, mule, <i>Hemionus odoniscus</i>		182	2.86	5.48				207				Kaibab Forest, Ariz.
86	3	M	" "			2.30	5.25				250				Kaibab Forest, Ariz.
87	1	F	" "												
27A	1	M	Dik-dik, <i>Rhynchotragus kirki</i>	4.57	37	0.73	0.56	36.8	93.2		21.4	44.4			Maji Moto, Africa
568	1	M	Elk, <i>Cervus canadensis</i>	13.61	194.2	6.14	2.38	131.1	374		73.4	319			Zoo, Cleveland, Ohio
136	1	F	" "			9.5	8.85				365				Zoo, Cleveland, Ohio
24	2	M	Gazelle, Thomson's, <i>Gazella thomsoni</i>	24.37	91.8	1.83	2.0	245	525	26.6	105	280			Maji Moto, Africa
54	1	F	" "	2.430	54.61	0.46	1.04	31.7	60.61	12.35	16.5	74.4		380	Infant, Maji Moto Africa
32A	1	M	Giraffe, <i>Giraffa camelopardalis tippelskirchi</i>	1,220	700	64.70	78.12	4,990	19,050	127	2,208	12,060	2,266	130,000	Maji Moto, Africa
1259	1	M	Goat, <i>Capra hircus</i>	27.66	115				525	29.55				1,466	Cleveland, Ohio
53	1	M	Hartebeest, <i>Conotragus (Kongoni), Bubalis cornei</i>	134	275	1.83	9.61	875	1,525	56.36	387	1,850	625	14,540	Moto Umbo, Africa
142A	1	F	Hippopotamus, <i>Hippopotamus amphibius</i>	543	540	32	53.35	1,610	14,060	35.02	1,175	4,910		83,000	Juvenile, Maji Moto, Africa

143	1	F	"	"	1,351	723	119	61.10	4,536	23,550	42.70	3,160	11,340	3,175	374,000	Adult, Maji Moto, Africa
143	53*	M	Hogs, <i>Sus scrofa</i> .	102.06	6.83	4.99	303.5	1,488.3	237.83	117.74	1,817	Average age, 236 days. Standard-bred castrates
143	36*	F	"	102.06	7.52	4.99	324.39	1,547.3	264.09	138.64	1,988.07	Age 241 days. Standard - bred young sows
143	30*	"	102.06	6.46	5.44	297.5	1,389.5	246.45	121.71	1,467.7	Ft crossbred. Average age, 252 days
176	2	F	Hogs, wild, <i>Sus scrofa</i>	8.42	2.71	Cumberland Island, Fla.
176	2	M	"	5.78	2.69	Cumberland Island, Fla.
180	5	Hogs, domestic, <i>Sus scrofa</i>	105	14.25	4.16	229	Cleveland, Ohio
180	194	"	16.7	3.05	232	Cleveland, Ohio
180	126	2	F	Lexington, Ky.
1377	5	M and F	Pigs, full-term fetuses.	1.419	30.3	0.45	0.27	14.25	43.0	3.29	10.47	25.66	1.06	Lexington, Ky.
1379	1	M	Pig, sboat, <i>Sus scrofa</i> .	4.76	51.2	0.74	0.37	52.1	184.6	4.05	32.8	98.7	12.5	Lexington, Ky.
1382	1	F	"	13.15	86.2	3.5	124.5	392.5	5.1	67.4	411.7	29.0	Lexington, Ky.
1384	1	M	"	104.5	5.6	9.3	147.3	903.8	6.2	130.8	1358	Lexington, Ky.
1419	1	M	"	7.60	54	1.6	2.0	469	284	7.0	54.0	128	Lexington, Ky.
1385	1	F	Pig	113.2	123.9	10.8	15.6	452	2,334	7.3	395.0	609.7	173.3	Lexington, Ky.
161	3	2	Impala, <i>Aepyceros melampus</i> .	37.86	149	5.67	3.82	270.05	605	44	162.5	510	210	5,800	Maji Moto, Africa
161	13	2	"	57.61	175	5.04	5.36	378	855	47.12	225	730	Maji Moto, Africa
106	1	F-P	"	5.67	4.62	Maji Moto, Africa

* Data furnished by the Bureau of Animal Industry, U.S. Department of Agriculture.

1394)	5	F	Lambs	8.55	71.5	4.29	6.03	85.0	237.2	13.7	69.5	180.5	27.0	About 1 month old. Lexington, Ky.
1396															
1408															
1421															
1424															
1409															
1422	4	M	" "	15.76	88.6	2.0	3.0	158.7	531.8	17.6	106.3	543.5	36.2	Lexington, Ky.
1425															
1427															
1393															
1400															
1402	7	F		52.1	106.5	10.2	8.3	276.7	957	30.49	159.8	704.8	119.6	Lexington, Ky.
1406															
1425															
1426															
25)	2	M	Steinbok, <i>Raphiterus</i>												
141)			<i>campestris neumanni</i>	8.62	49.5	1.22	1.35	72.2	175	14.87	38.51	150	550	Maji Moto, Africa
56	1	M	Warthog, <i>Phacochoerus</i>												
			<i>aethiopicus</i>	65.32	125	3.6	8.24	325	1,500	17.91	300	550	9,560	Maji Moto, Africa
34	1	M	Wildebesset, <i>Gnu tauri-</i>												
			<i>nus albotubatus</i>	215.49	451	14.51	7.45	1,325	2,000	425	3,200	Maji Moto, Africa
181	1	M	" "	208.65	450	7.36	9.4	1,300	2,540	570	2,500	37,194	Maji Moto, Africa

UNGULATES—ODD-TOED

786	3	F	Thoroughbred fetus, <i>Equus caballus</i>	13.00	150	4.18	2.21	111.3	702	99	444.3	82.5	Average, 91 days, premature. Ken- tucky
788	5	F	"	28.47	254.4	13.23	14.89	331.5	902.2	37.14	245.0	895.7	139.0	Average, 46.4 days, premature. Ken- tucky
890	5	M	"	27.30	273.9	12.28	4.66	275.9	699.5	51.48	257.4	1,374	162.5	Average, 54.4 days, premature. Ken- tucky
	11	F	"	47.68	333.9	17.54	8.10	472	1,634	42.82	321.3	1,526	335.1	Average, 14.6 days, premature. Ken- tucky

UNGULATES—ODD-TOED.—(Continued)

Catalogue number	Number of	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lungs, gm.	Spleen, gm.	Stomach and intestines, gm.	Remarks
1415	15	M	Thoroughbred fetus, <i>Equus caballus</i>	38.91	317.3	14.80	6.26	458.2	1,266	45.95	275.6	1,179	235.8	Average, 16 days, mature. Kentucky
1234	19	F	Thoroughbred foals.....	54.32	366.5	16.80	10.38	606.4	1,651	54.80	405.7	1,414	306.6	Average, 5.6 days old. Kentucky
1241	18	M	"	52.45	370.1	17.57	9.34	565	1,592	48.5	323.5	1,366	319	Average, 3.1 days old. Kentucky
815	3	M	"	93.89	425.3	15.23	14.43	970	3,386	56.8	859.3	1,427	610.3	Average, 33.5 days old. Kentucky
1236	4	F	"	116.77	470.2	22.6	15.20	1,125	3,704	67.5	812.2	1,393	838.5	Average, 83 days old. Kentucky
1244	8	M	" colts...	285.13	582.8	26.55	18.77	1,999	8,193	71.09	767.7	299.6	1,700	Average, 9 months old. Kentucky
1466	3	M	"	298.0	595.0	21.51	21.85	2,453	4,560	83.2	1,363	2,741	Yearlings. Lexington, Ky.
1471	1	F	" colts..	222.0	535.0	36.5	20.7	1,790	3,790	885	2,070	Weanling. Lexington, Ky.
1470	1	F	"	354.0	570.0	28.9	21.9	3,010	93.3	1,520	3,280	Yearling. Lexington, Ky.
1231	2	F	" fillies....	380.11	616	36.9	32.3	2,653	3,452	81.5	1,168	2,969.5	3,379	Average, 12 months old. Kentucky
1349	5	M	" colts....	306.35	602.4	26.81	22.2	2,708	4,821	70.05	970.2	3,110	5,494	Yearling colts. Kentucky
1467	1	" gelding.	299.0	530.0	23.5	2,330	4,965	77.0	910	6,160	Yearling. Lexington, Ky.
1467	11	M	" geldings.	445.76	639	29.91	34.30	3,444	5,354	97.20	1,404	3,963	4,239	Average, 4 1/4 years old. Kentucky

1224	3	M	Thoroughbred colts...	433.92	621.4	26.50	27.71	3,438	3,931	89.90	1,207	3,659	4,190	Average, 2-3 years old. Kentucky
606	7	F	" fillies....	408.5	632	30.56	38.41	3,237	5,350	98.82	1,633	4,588	3,438	Average, 2-3 years old. Kentucky
1351	1	M	Thoroughbred stallion	431.0	47.5	76.7	5,270.0	73.4	3,580	6,170	Lexington, Ky.
1473	1	M	Thoroughbred stallion	442.1	735	36.35	25.02	5,250	7,060	91.75	1,892	4,995	5,350	Whitney Stables, Lexington, Ky.
676	1	M	Thoroughbred stallion	521.52	808.5	33.40	46.62	4,455	1,549	3,968	Whitney Stables, Lexington, Ky.
686	1	M	Thoroughbred colt by "Equipoise".....	262.1	611	20.04	13.20	2,038	4,518	71.31	809	2,240	1,850	Whitney Stables, Lexington, Ky.
661	1	F	Thoroughbred mare "Brown Eyes".....	548.87	650	26.45	60.78	4,435	6,904	117.13	2,220	4,085	5,045	Goodloe Stables, Lexington, Ky.
636	1	F	Hunter "Roxanne".....	402.65	690.11	24.45	47.32	3,643	5,220	112.60	1,200	10,120	1,760	28,110	Little Mountain, Ohio
5	5	M	Thoroughbred stallions.....	485.31	706.7	32.15	33.03	4,688	5,685	106.34	1,971.7	7,154	3,474	Average, 17.3 years old. Kentucky
1468	1	M	Thoroughbred stallion.	531.0	620.0	24.0	44.0	4,800	6,670	106.3	1,930	4,800	13 years old. Lexington, Ky.
694	10	F	" mares..	443.36	637.7	29.76	43.5	3,663	6,176	105.0	1,667	4,758	3,856	Average, 19.1 years old. Kentucky
694	1	M	Arabian stallion "Nureddin".....	461.76	618	46.80	26.80	3,909	6,375	112.24	1,512	5,080	3,000	27 years old. Portsmouth, Ohio
1287	1	M	Arabian stallion "Mirage".....	362.80	573	34.95	42.17	3,275	4,670	108.08	1,108	6,475	1,900	30 yrs. old. Portsmouth, Ohio
1221	1	F	Arabian mare "Gue-mura".....	711.4	80.00	3,230	107.8	Franklin, Tenn.
1306	1	M	Burro gelding	199.58	392	14.43	24.2	1,184	3,770	844	1,462	507	25 years old. Kentucky

UNGULATES—ODD-TOED.—(Continued)

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
707 711	2 M	"Charcoal" horses	122.98	478	4.80	16.64	850	1,953	84.31	813	1,320	280	Average, 4 years old. Guatemala City, C. A.
708	1 F	Burro	150.73	410	10.32	16.34	825	1,266	69.30	1,575	1,260	590	Guatemala City, C. A.
1242	1 M	Grade draft	70.76	248	11.2	7.9	546	1,197	40.0	230	916	524	Foal. Kentucky
659 660	2 F	Grade pony	184.16	525	10.49	12.98	1,165	2,100	67.47	420	1,348	458	1 year old. Kentucky
664	1 F	Draft horse	521.64	655	24.30	52.51	3,290	6,920	105.92	1,510	4,125	1,807	12 years old. Kentucky
1317	1 M 10 M	Hackney pony Horses, Panama	362.87 279	504 452	29.6 10.77	21.2 25.75	1,427						Urbana, Ill.
31	1 F	" "	262	468	12.77	25.62							Average 12 years old. Panama gelding work horses
21	1 M and F	" "	230.9	520		35.45	1,843	4,277		942	3,627	940	Average 14 years old. Panama mares
3	3 M	Mules, Panama, <i>Equus asinus</i>	211	371	8.66	24.6							Average 13.3 years old. Panama
4	1 F	" "	291	478	9.75	35.5							Average, 20 years old. Panama
1	1 M	" "	42.64	227			397	1,191		227	628	283	Panama colt
4	4 M and F	" "	279.2			42.53	2,048	3,594		513	4,026	766	Panama
702	1 F	Mule	249.47	543	11.3	47	2,144	6,301		1,049		802	1 year old. Kentucky
1267	1 F	" "	444.52	543	18.98	45.1	3,604	5,342	124.0	964	5,678	1,802	25 years old. Kentucky

600	1	M	Percheron stallion.....	635.04	662	40.94	39.23	5,600	8,520	136.7	1,700	5,710	3,430	14 years old. Ohio
601	1	F	Percheron mare.....	771.40	650	56.55	37.40	4,700	6,725	137.4	1,750	5,400	1,550	23 years old. Ohio
635	1	F	Polo pony.....	380.75	602	52.10	24.23	3,570	4,835	115.92	950	8,016	1,250	25 years old. Cleveland, Ohio
1307	1	F	Pony.....	376.48	604	20.02	28.00	2,607	5,012	96.5	1,894	2,558	3,846	18 years old. Kentucky
791	1	F	Saddle-bred fetus.....	19.50	226	7.2	2.6	181.5	913	1,038	141	71 days premature.
1245	1	F	Saddle-bred foal.....	118.8	475	12.8	10.2	894	2,706	56.0	735	536	3 months old. Kentucky
1296	1	F	" weanling.	181.4	402	1,418	64.0	2,981	6-7 months old. Kentucky
800	2	M	Saddle-bred colts.....	300.5	588	18.43	17.33	1,658	4,397	87.65	1,033	3,457	1,079	1 year old. Kentucky
1295	2	M	" geldings..	335.68	569	16.95	20.70	2,199	4,616	84.48	929	3,189	2,010	1 year old. Kentucky
1458	1	Saddle horse gelding..	449.0	540.0	14.57	40.5	3,495.0	7,220	110.0	1,520	3,550	3,475	Portsmouth, Ohio
1348	1	M	Shetland pony gelding.	242.67	560	15.25	23.5	2,195	3,975	104.0	870	3,740	1,380	20 years old. Kentucky
1449	1	F	Shetland pony.....	272.19	553.2	87.6	23.2	2,508.0	4,543	93.0	1,307	1,871	Cleveland, Ohio
273	1	M	" stallion.....	150.35	496.11	14.70	16.29	1,375	1,805	4,111	Little Mountain, Ohio
803	1	F	Standard-bred fetus...	31.75	243	11.9	6.7	402	1,052	196	921	84	About 60 days premature. Kentucky
1240	1	M	Standard-bred foal....	92.98	400	14.6	10.1	971	2,400	86.0	624	1,489	330	3 months old. Kentucky
636	1	F	Hunter (thoroughbred).....	402.65	600	24.45	47.32	3,648	5,220	112.6	1,200	10,120	1,760	15 years old. Ohio
603	1	M	Western gelding.....	426.38	562	25.59	35.37	3,457	5,338	107.0	1,196	4,005	5,760	23 years old. Ohio
8A	1	M	Rhinoceros, <i>Rhinoceros bicornis</i>	764	655	53.05	168.66	4,800	14,310	22.56	3,000	7,350	2,720	Maji Moto, Africa
1464	1	F	Tapir, <i>Tapirella bairdii</i>	53.06	159.4	7.44	11.02	540.0	815	14.88	462	2,068	Panama Canal Zone
.....	1	Tapir, <i>Tapirella bairdii</i> (Gill).....	8.60	2.0	74	220	92	162	84	Juvenile, Panama

UNGULATES—ODD-TOED.—(Continued)

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
686	1 M	" " Zebra, <i>Equus quagga</i> <i>gravi</i>	14.26	85	3.0	121	483	167	318	172	Adult, Panama
35A	1 M	" " "	20.48	14.77	6.24	330	937	39.5	90.54	655	135.8	Fetus, Zoo, Cleveland, Ohio
634	1 F	" " "	7.900	125	3.04	1.43	75	275	53.56	300	Embryo, Maji Moto, Africa
179A	1 F	" " "	43.09	413	29.2	9.6	581	1,275	166.4	740	156.1	Infant, Zoo, Cleveland, Ohio (goiter)
638	1 M	" " "	56.59	410	10	4.95	515	950	262	1,025	605	6 weeks old, Maji Moto, Africa (goiter)
20A 160A 163A 668	2 M 1 F-P 1 M	" " "	78.02	494.4	48.6	11.5	660	357.3	Zoo, Cleveland, Ohio (goiter)
		" " "	254.99	541	20.08	23.08	1,925	4,037	94	850	2,025	1,170	Maji Moto, Africa
		" " "	237.1	555	17.34	27.8	1,970	4,400	89	900	2,790	Maji Moto, Africa
		" " "	317.5	642	36.0	44.1	2,231	6,336	103	1,239	1,121	Jungle bred, 6 years old, Zoo, Cleveland, Ohio

PROBOSCIDEA AND HYRACOIDEA

Catalogue number	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.
148A	1 M	Elephant, <i>Loxodonta africana knochenkavi</i>	6,654	5,712	860	940	26,060	107,670	116.15	18,180	138,790	924,000
142	1 F	Elephant, <i>pygmy</i> , <i>Loxodonta cyclotis</i>	84	5,200	Zoo, New York City
149A	1 M	Hyrax, <i>Heterohyrax brucei</i>	0.750	12.37	0.081	0.161	3.63	31.53	6.45	5.532	255

SIRENIA

1475	1	M	Manatee, <i>Trichechus manatus</i>	424.0	351.0	57.51	1,250.0	5,500	8.0	3,050	Miami, Fla.
	1	F	"	557.92		78.87	1,247	6,236	59.9	3,741	Miami, Fla.

PRIMATES

	1	F	Baboon, <i>Papio cynocephalus</i>	7.900	140	0.437	2.30				Juvenile, Department of Physiology, Yale University
22A	1	M	"	19.51	175	1.8	2.05	13.18	70.92	175	Moto Umbo, Africa
93A	1	F	Monkey, gray, <i>Cercopithecus mitis tibonensis</i> (Lonnberg)....	1.22	50.3	0.172	0.22		7.84	9.98	Maji Moto, Africa
92A	1	M	"	2.9	61.46	0.39	0.41	9.94	8.71	14.39	Maji Moto, Africa
4A	1	M	"	4.55	66.6	0.15	0.902		20.63	41.63	Maji Moto, Africa
	10	M and F	Howler, black, <i>Alouatta palliata inconsona</i> (Goldman)...	0.673	42.88		0.588		6.19	9.88	Infant, Panama
	3	M and F	"	2.663	46.1		0.67		15.4	22.7	Juvenile, Panama
	28	M	"	6.174	50.34		1.16		35.95	38.68	Adult, Panama
	2	F	"	4.309	54.25	0.45	0.8				Juvenile, Panama
	2	F	"	6.577	54.05	0.55	0.95				Adult, Panama
	2	M	"	7.998	53.45	0.55	0.95				Adult, Panama
	2		Howler, brown, <i>Alouatta palliata palliata</i> .	0.420	37		0.45		3.2	6.5	Infant, Panama
	5	M and F	"	1.209	37.6		1.6		12.5	11.5	Juvenile, Panama
	6	M and F	"	3.119	42.3		1.5		21.33	28.3	Adult, Panama

PRIMATES.—(Continued)

[illegible]

5	F	"	"	5.143	110.6	0.798	1.65								Juvenile, Panama
8	M	"	"	4.999	94.7	0.64	2.0								Juvenile, Panama
13	M	"	"	7.787	117	0.90	2.05								Adult, Panama
14	F	"	"	8.912	102.9	1.04	1.95								Adult, Panama
2		Spider, black, <i>Ateles</i> <i>dartensis</i> (Goldman).	"	0.407	58.0		0.75	2.75	19		4.5	6.5	2.0		Infant, Panama
18	M	"	"	1.926	88.6	0.785	1.06	7.65	74.5		11.6	17.3	8.6		Juvenile, Panama
11	F	"	"	9.163	108.8	1.28	2.12								Adult, Panama
6	M	"	"	8.89	118.4	1.42	2.23								Adult, Panama
133	M	Squirrel (marmoset), <i>Leontocobus Geoffroyi</i> (Pucheran)	"	0.191	9.67		0.56	1.34	9.33		1.87	3.13	1.16		Infant, Panama
4	F	"	"	0.340	10.4	0.10	0.25								Juvenile, Panama
3	M	"	"	0.453	11.1	0.133	0.23								Juvenile, Panama
19	M	"	"	0.475	11.04		0.53	3.02	16.53		2.89	3.91	1.38		Juvenile, Panama
8	M	"	"	0.793	19.9		0.63	3.91	25.41		4.24	8.48	1.65		Adult, Panama
8	M	"	"	0.903	24.00	0.11	0.30								Adult, Panama
2	M	Sykes, <i>Cercopithecus</i> ...	"	4.937	60.7	1.14	0.878	29.97	119.6		10.70	21.35	85.16		Maji Moto, Africa
2	M	Vervet, <i>Cercopithecus</i> ...	"												
2	M	<i>aethiops</i> (Neumann)	"	4.185	57.75	0.175	0.735	19.98	94.40	8.83	15.89	17.01			Maji Moto, Africa
1	F	"	"	1.225	50.3	0.172	0.220	6.56	29.55		7.84	9.98		250	Juvenile, Maji Moto, Africa
4	F	Whiteface, <i>Cebus cap-</i> <i>cinus innuus</i> ...	"	2.718	71.6	0.4	1.43								Panama
5	M	"	"	3.633	73.3	0.36	1.23								Panama
6	F	"	"	1.252	60.8	0.26	0.70								Juvenile, Panama
7	M	"	"	1.725	75.5	0.34	0.61								Juvenile, Panama
14	M	"	"	3.101	72.18		1.06	18.6			14.3	34.07	11.3		Adult, Panama
6	M	"	"	1.317	66		0.067	7.53			8.56	20.44	5.7		Juvenile, Panama
27	M	"	"	0.560	53.38		0.568	3.06			4.04	7.93	2.10		Infant, Panama

99A
70A

98A

PRIMATES.—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	
	60	M and F	Yellow Titi, <i>Scotomys orstedii orstedii reinhardtii</i>	0.607	19.9	0.15	0.63	3.68	25.6	3.99	7.20	0.9	Adult, Panama
	3	M	"	0.907	25.3	0.15	0.447	Panama
	2	"	0.167	19.4	0.20	0.85	7	1.3	2.5	0.3	Infant, Panama
	2	"	0.24	22	0.45	1.25	12	2.5	4.9	0.65	Juvenile, Panama
	3	F	"	0.603	25	0.16	0.323	Adult, Panama

ANTHROPOIDS															
	1	F	Chimpanzee, <i>Troglodytes niger</i>	3.8	Yale University Department of Physiology
215	1	M	"	25.75	430.5	10.1	5.0	184.6	Yale Univ. Department of Physiology
218A	1	M	"	52.16	440	4.85	8.93	250	1,210	210	600	6,200	Emaciated specimen from New York
219A	1	F	"	43.99	325	4.55	8.4	219	Budonga Forest, Northern Province, Uganda, Africa
	1	M	Gorilla, <i>Gorilla gorilla</i>	181	6*	35 est.	Budonga Forest, Northern Province, Uganda, Africa

* Estimated

1291	1	M	Chinese.....	57.2	1,248	21.54	10.1	Age 70 years, Australia
1320	1	M	"	1,297	13.3	5.35	Age 70 years, Australia
1328	1	M	"	1,268	11.4	9.9	Age 70 years, Australia
1403	1	M	"	1,268	13.99	7.88	Age 70 years, Australia
1340	1	M	Hawaiian.....	83.89	1,480	16.7	Age 70 years, Australia
745	1	M	Maya Quiche Indian.....	95	1,235	16.7	Age 70 years, Australia
767	1	M	"	42	1,270	35	15	220	1,040	185	1,315	Age 35. Death from tuberculosis
768	1	M	"	43.4	1,375	80	14	210	1,270	170	755	Age 35. Death from septicaemia (got-ter)
1109	1	M	"	49.9	1,400	30	10	240	Age 32. Death from double pneumonia
1324	1	M	"	36.3	1,280	11.1	5.6	155	Age 45. Death from cachexia
1336	1	M	"	45	1,190	108	10	226	Age 32. Death from pneumonia (got-ter)
1341	1	M	"	37	1,100	10	5.0	159	Age 17. Death from cachexia
1357	1	F	"	45.8	1,000	10	10	225	Age 28. Death from cachexia
751	1	M	Filipino	43.09	1,109	25.1	200	Age 39. Hawaii
752	1	M	"	40.83	1,513	16.8	9.3	Age 53. Hawaii
753	1	M	Aborigine, Australian.....	76.2	1,348	36.5	4.2	Age 66. Australia. Death from pneumonia
1312	1	M	Negro, American.....	86.2	1,365	19.8	16.7	365	1,520	Age 41. American born
1255	1	M	"	71.2	1,280	18.2	11.8	465	1,500	Age 24. New York
1454	1	M	"	72.87	1,050	34.2	11.4	320	1,980	178	Age 45. New Orleans, La. (2) and Cleveland, Ohio
754	4	M	"	73	1,365	31.77	12.69	389	250	(2)
755	8	M	"	78.5	1,640	37.3	16.4	331	2,010	292	Age 25. Czechoslovakian descent
1316	1	M	White, American.....	Age 13. Denmark
1327	1	M	Dane.....	36	1,370	14	11	220	Age 47. Denmark
1353	1	F	"	61	1,200	17	13	300	Age 47. Denmark

ANTHROPOIDS.—(Continued)

Catalogue number	Number of animals	Sex	Common and scientific name	Body wt., kg.	Brain, gm.	Thyroid, gm.	Adrenal, gm.	Heart, gm.	Liver, gm.	Eyes, gm.	Kidney, gm.	Lung, gm.	Spleen, gm.	Stomach and intestines, gm.	
1333	1	F	Dane	46	1,160	23	14	260	Age 68. Denmark
1336	1	F	"	43	1,240	14	18	320	Age 65. Denmark
1336	1	F	"	63	1,180	17	14	450	Age 78. Denmark
1324	1	F	"	43	1,350	15	13	220	Age 50. Denmark
1322	1	F	"	44	1,300	10	310	Age 44. Denmark
1322	1	F	"	46	1,140	15	410	Age 60. Denmark
1321	1	M	"	51	1,500	24	380	Age 55. Denmark
1325	1	M	"	83	1,420	29	520	Age 68. Denmark
1328	1	M	"	56	1,570	47	19	380	Age 28. Denmark
1329	1	M	"	61	1,490	26	17	410	Age 39. Denmark
1331	1	M	"	51	1,310	27	15	290	Age 55. Denmark
1314	1	M	White, American.....	81.6	1,350	42	12	370	1,200	320	Age 22. German descent
763	1	M	"	1,450	42.63	9.42	330	1,500	110	1,280	100	Age ? Irish descent
1311	1	M	"	79.4	1,274	35	12.9	390	1,970	Age 54. Polish descent
1313	1	M	"	81.6	1,130	20	16.6	400	1,730	Age 54. Polish descent
1459	1	M	"	58.97	1,330	23	11.4	280	1,460	310	130	Irish, New York
1444	1	M	"	58.97	1,310	31	22.1	308	1,100	298	Jewish, New York
1445	1	M	"	59.42	1,410	63.4	12.6	265	1,505	251	Bohemian, New York (goiter)
1433	1	M	"	61.24	1,310	24.6	10.5	250	1,625	208	New York
1499	1	M	"	63.50	1,390	18.21	7.9	310	1,330	292	360	135	New York
1490	1	M	"	65.77	1,350	31.7	13.3	270	1,310	260	110	Irish, New York
1453	1	M	"	66.93	1,475	11.84	12.5	Honolulu, T. H.
1461	1	M	"	70.30	1,260	41.3	13.7	320	1,750	280	270	Italian, New York
1462	1	M	"	70.30	1,240	27.3	12.9	310	1,730	310	620	150	Jewish, New York
1463	1	M	"	72.57	1,260	21	13.6	260	1,600	320	Jewish, New York
610	1	M	Pole, immigrant.....	74	1,377	23.92	10.94	382	Age 41. Cleveland, Ohio
769	1	M	White, American.....	50	1,480	48.47	14.96	325	1,800	350	100	Age 45. Scottish descent, New York
1315	1	M	"	85.8	1,310	23.6	17.6	340	1,780	310	Age 30. Swedish descent

GLOSSARY

- Abdomen.** The body division posterior to the diaphragm in mammals.
- Abducens.** Leading away from; the sixth cranial nerve.
- Abduction.** Movement away from the midplane of the body.
- Abomasum.** The last of the four divisions of the ruminant stomach.
- Aboral.** Away from the mouth.
- Acanthias.** Spiny; species name of the common dogfish.
- Acentrous.** Without a centrum.
- Acetabulum.** Literally vinegar cup; a socket in the innominate bone for the head of the femur.
- Acinose.** Grape-like; designates certain types of glands.
- Acinus.** A terminal sac in lung or in glands.
- Acipenser.** The genus name for the sturgeon.
- Acoustic.** Pertaining to hearing.
- Acrania.** The protochordates without a brain case.
- Acrodon.** A type of dentition in which the teeth are fused with the medial margins of the jaws.
- Acromegaly.** Overgrowth of the bones, particularly of points like chin or cheek bones, due to pathology of the anterior lobe of the pituitary gland.
- Acromion.** Top of the shoulder; the process on the scapular spine.
- Actinopterygii.** Fishes with fin rays.
- Actinotrichium.** Hair-like ray of the fish fin.
- Adaptation.** Becoming fitted structurally and functionally to certain conditions.
- Adduction.** Movement toward the midline of the body.
- Adenoid tissue.** Glandular tissue of lymphatic character.
- Adipose.** Pertaining to fatty tissue.
- Adrenal gland.** An endocrine gland in close proximity to the kidney.
- Adsorption.** Attachment of a thin molecular layer of substance to the surface of a solid, in contrast to absorption.
- Afferent.** Toward.
- Agnatha.** Without jaws; the cyclostomes.
- Air sac.** A respiratory sac in birds.
- Allantois.** The embryonic respiratory organ.
- Alveolus.** A small outpocketing.
- Ammocoetes.** The larval stage of the lamprey.
- Amnion.** The embryonic covering membrane of animals above the amphibian level.
- Amphibian.** Pertaining to a class of vertebrates, *e.g.*, the frog.
- Amphicelous.** Having a concavity at each end; a type of vertebra.
- Amphiplatyan.** Having flat ends; a type of vertebra.
- Amputilla.** Rounded, flask-like expansion, especially such enlargements in the inner ear.
- Amylopsin.** A digestive enzyme that breaks down starch produced by the pancreas.

- Analogous.** Similar in function although of different origin.
- Anastomosis.** A joining of vessels, nerves, or other structures.
- Anconeus.** A small extensor muscle at the elbow, derived from the triceps.
- Ankylosis.** A fusion of a joint through bone deposition.
- Anlage.** A primordium, or first embryonic appearance of a structure.
- Anterior.** Toward the head.
- Anura.** Literally without a tail; an order of tailless Amphibia.
- Apoda.** Without feet; a group of amphibians without appendages.
- Aponeurosis.** A fascial tendinous sheath or layer serving as a muscle attachment.
- Apophysis.** A process on the vertebra with which the rib tubercle articulates.
- Arachnoid.** A delicate, spiderweb-like network.
- Arboreal.** Tree dwelling.
- Archaeopteryx.** A reptile-like bird from the Jurassic period.
- Archenteron.** The original, endodermally lined embryonic gut cavity.
- Archipterygium.** The primitive appendage of aquatic vertebrates.
- Arytenoid.** Small, pitcher-shaped cartilage in the larynx.
- Astragalus.** Large ankle bone articulating with the tibia.
- Atlas.** The first cervical vertebra.
- Atriopore.** Opening of the gill chamber to the exterior in Amphioxus.
- Atrium.** One of the heart chambers; synonymous with auricle.
- Axilla.** The armpit.
- Axon.** A nerve cell process.
- Azygous.** An unpaired vein in the thorax.
- Balanoglossus.** A genus of Hemichordata.
- Barb.** A point.
- Bartholin glands.** Vaginal glands.
- Basal ganglia.** The striate body in the ventrolateral telencephalic wall.
- Basalia.** The proximal appendicular cartilages of the cartilaginous skeleton.
- Basi.** Prefix meaning "at the base of."
- Basibranchial.** At the base of the gills.
- Basicranial.** At the base of the skull.
- Basidorsalia.** Paired elements associated with vertebral development.
- Basihyal.** The most ventral segment of the hyoid arch.
- Basilar membrane.** A membrane in the organ of Corti.
- Basilingual plate.** Visceral skeletal element supporting the tongue.
- Basioccipital.** That part of the occipital bone surrounding the foramen magnum.
- Basiventralia.** Paired elements associated with vertebral development.
- Basophilic.** Having affinity for basic stains.
- Betz, cells of.** Giant cortical motor cells.
- Biceps.** Having two heads; designates a muscle of arm and of thigh.
- Bicuspid.** Having two cusps; designates premolar teeth and left atrioventricular heart valves.
- Bilateral.** Relating to a type of symmetry in which one side is the mirror image of the other.
- Biogenesis.** The concept that only life begets life.
- Biramous.** Consisting of two approximately equal elements.
- Bladder.** A sac or vesicle.
- Blastocele.** The cavity in the embryonic blastula.
- Blastula.** An early stage in embryonic growth before germ layers differentiate.

- Blindworm.** An apodous amphibian.
- Bowfin.** Fish belonging to genus *Amia*.
- Bowman's capsule.** That part of the nephron surrounding the glomerulus.
- Brachium.** The arm.
- Brachium conjunctivum.** The superior cerebellar peduncle.
- Brachium pontis.** The middle cerebellar peduncle leading from pons to cerebellum.
- Brachydont.** A type of tooth with a long neck.
- Branchia.** Gills.
- Branchiostegal.** Pertaining to the membrane or to the rays attached to the ventral margin of the operculum in some bony fishes.
- Branchiostoma.** The original genus name for *Amphioxus*.
- Broad ligament.** Mesenterial fold that supports the oviduct and uterus.
- Broca's area.** Gyrus on medial surface of cerebral hemisphere.
- Bronchioles.** The small air tubes resulting from repeated division of the bronchi.
- Bronchus.** One of the primary divisions of the trachea.
- Brunner's glands.** Glands characteristic of the duodenum.
- Brünn man.** An archaic Mediterranean subrace of the Upper Paleolithic.
- Buccal.** An adjective which refers to the cheek or the cavity of the mouth.
- Buccinator.** Literally a trumpeter; a cheek muscle.
- Bud.** Limb; the primordium of a limb in embryonic development.
- Bulbourethral gland.** Cowper's gland; one of the genital glands.
- Bulbus.** The expanded bulb-like origin of the aorta.
- Bulla.** The expanded petrous bone at the base of the middle ear in many mammals.
- Bundle of His.** Nerve bundle in the heart, a part of the conduction system.
- Bunodont.** A type of cone-pointed tooth, characteristic, for example, of pig dentition.
- Burdach, column of.** An ascending nerve tract in the spinal cord.
- Bursa.** A sac-like cavity lined with a synovial membrane.
- Bursa Fabricii.** A cloacal evagination in birds.
- Buttocks.** Muscle-fat pads covering the ischial tuberosities prominent in man but relatively more prominent in woman.
- Calcaneum.** The heel bone.
- Calcareous.** Pertaining to lime salts or deposits.
- Calcarine fissure.** A cleft on the medial side of the occipital cerebral lobe characteristic of primates.
- Calyx.** A cup-like recess in the renal pelvis.
- Canaliculus.** A minute canal uniting the lacunae in compact bone.
- Canine tooth.** A tooth lateral to the incisors and prominent in carnivores.
- Capillary.** A minute blood vessel.
- Capitate bone.** One of the wrist bones.
- Capitular head.** The head of a rib.
- Carapace.** The dorsal hard shell of the turtle.
- Cardiac.** Referring to the heart.
- Carina.** The keel of a bird.
- Carinatae.** Flying birds having a well-developed keel.
- Carnassial teeth.** The last upper premolar and first lower molar in carnivores—they produce a shearing action.
- Carnivora.** A flesh-eating order of mammal.

- Carotid body.** A small gland at the junction of the external and internal carotid arteries, containing chemoreceptors.
- Carotid sinus.** Dilated section of the internal carotid artery at its origin.
- Carpus.** Wrist.
- Castration.** Removal of testes or ovaries.
- Catabolism.** Destructive metabolism.
- Catarrhines.** Old World, narrow-nosed monkeys.
- Caudad.** Toward the tail.
- Cauda equina.** The distal termination of the spinal cord.
- Cava.** The vena cava.
- Cecum.** A pouch into which colon, ileum, and appendix open.
- Celiac.** Pertaining to the abdominal cavity.
- Celiac axis.** Large artery in the abdomen.
- Celiac plexus.** Sympathetic nerve plexus in the abdomen.
- Celom.** Body cavity.
- Centralla.** A group of four centrally placed wristbones in the primitive limb.
- Centrum.** The body of a vertebra collectively forming the supporting column.
- Cephalic.** Toward the head.
- Cephalization.** Head or brain development.
- Cephalochordata.** A division of the Protochordata.
- Cerebellum.** The fourth major brain division, the balancing center.
- Cerebral commissure.** Transverse nerve fiber tract connecting the cerebral hemispheres.
- Cerebrum.** A major brain division developed from the telencephalon.
- Cerumen.** The wax-like secretion of the ear.
- Cervical.** Pertaining to the neck.
- Cervix.** A constricted part of an organ, *e.g.*, the cervix of the uterus.
- Cetacea.** An order of aquatic mammals including porpoises and whales.
- Chemoreceptor.** A sensory receptor excited by chemical agents.
- Chiasma.** Crossed nerve fibers, *e.g.*, the optic chiasma.
- Chiropterygium.** The limb skeleton of land animals.
- Choana.** A funnel-shaped cavity.
- Cholecystokinlin.** A hormone secreted by intestinal mucosa which activates the gall bladder.
- Choledochal duct.** The common bile duct.
- Cholesterol.** A fat-like higher alcohol present in animal fats.
- Chondrichthyes.** Cartilaginous fishes.
- Chondrocranium.** The cartilaginous skull.
- Chorda tympani.** A taste and secretory branch of the facial nerve.
- Chordae tendineae.** Tendons in the heart connecting muscle slips to the heart valves.
- Chorioid.** A vascular coat.
- Chorion.** The outer protective envelope of the amniote embryo.
- Choroid.** Resembling the skin; the pigmented vascular coat of the eye.
- Chorology.** Science of the distribution of animals over the earth.
- Chromaffin.** Having affinity for chrome salts.
- Chromatin.** The highly stainable fibrillar material in the cell nucleus.
- Chromatophores.** Pigment cells.
- Chromosomes.** Rod-shaped bodies in cell nuclei; determiners of hereditary characteristics.

- Chyle.** Emulsified fat and lymph taken up by lacteals in digestion.
- Chyme.** The food mass as it leaves the stomach after gastric digestion.
- Cilia.** Fine, hair-like motile cell processes.
- Ciliary body.** The margin of the choroid process serving for the lens attachment in the eye.
- Ciliary muscle.** A muscle in the choroid process active in visual accommodation.
- Cinerea.** Gray substance of the nervous system.
- Cingulum.** A girdle of association fibers about the corpus callosum.
- Circumduction.** Circular movement of an extremity about a central pivot.
- Circumvallate papillae.** Large, cup-shaped taste papillae of the tongue.
- Cisterna chyli.** Expanded lower end of the thoracic duct for reception of chyle.
- Clasper.** Modified pelvic fin in male elasmobranchs adapted for copulation.
- Clavicle.** The collar bone.
- Cleithrum.** A supporting shoulder girdle bone in some fishes and fossil amphibians.
- Climatius.** A genus of Devonian fossil fish.
- Clinoid.** Bed-shaped.
- Clinology.** The science of the regression of animal organisms.
- Clitoris.** A small erectile body at the superior angle of the vulva in the female.
- Cloaca.** A common cavity into which open the urogenital tract and large intestine.
- Coccyx.** The caudal end of the spinal column.
- Cochlea.** The spirally wound tube of the inner ear.
- Collagen.** The organic substance of connective tissue and of bone.
- Colliculus.** One of the corpora quadrigemina.
- Colloid.** A type of distribution of matter in a dispersion medium.
- Colon.** The large intestine extending from cecum to rectum.
- Columella.** One of the amphibian ear bones.
- Commissure.** A band of nerve fibers uniting the cerebral hemispheres.
- Concha.** A shell; the hollow of the external ear; the nasal turbinal bones.
- Condyle.** The rounded articular end of a bone.
- Conjunctiva.** The membranous lining of eyelids that also covers the eyeball.
- Conus arteriosus.** The expanded right ventricle at the origin of the pulmonary artery.
- Coprodeum.** That division of the cloaca into which the intestine opens.
- Copula.** A junction; the basal branchial segments.
- Copulation.** Sexual intercourse.
- Coracoid.** The hook-like bony element fused with the scapula.
- Corium.** The dermal skin layer.
- Cornea.** The transparent layer of the eyeball covering the aqueous humor.
- Cornu.** A horn-like projection.
- Corona.** A crown, *e.g.*, the coronary artery.
- Corpora.** The plural of corpus; bodies.
- Corpora bigemina.** Paired eminences on the mesencephalon.
- Corpora-cavernosa.** Erectile bodies of the penis containing hollow spaces.
- Corpora quadrigemina.** Four eminences in the dorsal part of the mesencephalon.
- Corpus callosum.** Large commissure joining the brain hemispheres.
- Corpus cavernosum urethrae.** Spongy body surrounding the female urethra.
- Corpuscle.** A small body; blood cells; sense corpuscles.
- Corpus luteum.** The yellow body of the ovary.

- Corpus restiforme.** A lateral column in the medulla oblongata.
- Corpus striatum.** A body of white and gray nerve matter anterior to the thalamus.
- Cortex.** The outer layer of an organ.
- Corti, organ of.** The sound perceiving mechanism of the inner ear.
- Cortin.** The hormonal principle of the adrenal cortex.
- Cosmine.** A dentinal scale layer in crossopterygian and dipnoan fishes.
- Costal.** Pertaining to ribs.
- Cowper's gland.** A bulbourethral gland.
- Cranial.** Toward the head.
- Craniata.** Animals with brain cases.
- Cremaster.** A muscle that retracts the testes.
- Cretaceous period.** The chalk-forming and last period of the Mesozoic era.
- Cretinism.** A condition caused by lack of thyroid secretion, resulting in dwarfing and sometimes in idiocy.
- Cribriform plate.** The horizontal perforated plate of the ethmoid bone.
- Cricoid cartilage.** A ring-shaped cartilage of the larynx.
- Crista.** A crest.
- Cro-Magnon man.** A human race dating to the Magdalenian period.
- Crossopterygii.** An order of lobe-finned fishes.
- Crura.** Plural of crus. Leg or leg-like processes.
- Crypt.** A pit.
- Cryptorchidism.** A failure of the testes to descend into the scrotum.
- Ctenoid scale.** A type of scale with serrated or comb-like free margin.
- Cuneiform.** Wedge-shaped.
- Cusp.** The tapering projection of a tooth.
- Cutaneous.** Pertaining to the skin.
- Cutis.** The dermal skin layer.
- Cycloid.** Oval-shaped scales.
- Cyclops.** A fetal monster with a median eye.
- Cyst.** A sac.
- Cytogenous.** The production of cells or an agent responsible for their proliferation.
- Cytoplasm.** The cell protoplasm outside the nucleus.
- Decidua.** The membrane lining the uterus in gestation and constituting the afterbirth at parturition.
- Decussate.** To cross as in a chiasma.
- Deferens.** Carrying away from; the vas deferens.
- Deiters' cells.** Cells in the membranous cochlea.
- Deltoid.** A triangular-shaped shoulder muscle.
- Dendrite.** A branched process from a nerve cell.
- Dens.** Tooth.
- Dentin.** Tooth tissue which surrounds the pulp cavity.
- Derma.** The corium, or deep layer of the skin.
- Dermatome.** A segmental cutaneous area.
- Diaphragm.** A large muscle in mammals separating the thorax and abdomen.
- Diapophysis.** A lateral projection of the centrum for attachment of the upper head of rib.
- Diapsid.** Having two lateral skull fossae.

- Diarthrosis.** A joint movable in all directions.
- Diastema.** A gap.
- Diastole.** The stage of dilatation in the heartbeat.
- Diecious.** Sexually distinct or singly sexed.
- Diencephalon.** The 'tween-brain; the division between cerebrum and midbrain in man.
- Digastric.** Having two bellies; the digastric muscle.
- Digit.** A finger or toe.
- Digitigrade.** Balanced upon the toes.
- Dimorphism.** Having two forms.
- Diphycercal.** A type of tail in fishes which is equally divided above and below the caudal vertebrae.
- Diphyodont.** Dual tooth succession.
- Diploblastic.** Having two germ layers.
- Diploe.** Loose bony tissue between the outer and inner layers of the cranial bones.
- Diploid.** Normal paired chromosomes.
- Diplospondyl.** A double vertebra.
- Discus proligerus.** The granular zone surrounding the ovum in the follicle.
- Distal.** Away from the central or proximal part.
- Diurnal.** Adapted for day activity.
- Diverticulum.** A side pouch leading from a main tube.
- Dorsal.** Pertaining to the back.
- Ductus arteriosus.** The connecting channel between pulmonary vein and aorta functional in embryonic development.
- Ductus botalli.** The ductus arteriosus.
- Duodenum.** The first part of the small intestine.
- Dura mater.** The tough outer meningeal membrane covering the brain.
- Ecology.** The study of the relationships of organisms to their environment.
- Ectoderm.** The outer embryonic germ layer.
- Ectoparasite.** A parasite attacking the surface of the body.
- Edentate.** Without teeth.
- Effector.** A nerve end organ that distributes action impulses to a muscle or gland.
- Efferent.** Away from; vessels, ducts, or nerves conveying blood, secretions, or nerve impulses away from a given part or nerve center.
- Elasmobranchii.** A group of cartilaginous fishes with plate-like gills.
- Enamel.** White, hard substance that covers the dentin of the tooth.
- Endocardium.** The endothelial lining of the heart.
- Endocrine.** Pertaining to ductless glands that secrete hormones.
- Endoderm.** The innermost germ layer.
- Endolymph.** Fluid in the membranous labyrinth of the ear.
- Endometrium.** The mucous membrane lining the uterus.
- Endoskeleton.** The internal skeleton.
- Endostyle.** The ciliated groove on the floor of the pharynx of *Amphioxus* and *Ammocoetes*.
- Enteron.** The primitive gut cavity.
- Enzyme.** An organic catalytic compound active in digestion and in other physiological transformations.
- Eoanthropus.** Generic name of the "dawn man" of England.

Epaxial. Above the axis; structures dorsal to the lateral skeletogenous septum.

Ependyma. The membrane lining the central spinal canal and the brain ventricles.

Epi. A prefix meaning "upon."

Epibranchial. The penultimate dorsal element of a branchial arch.

Epicardium. The inner layer of the pericardial sac.

Epicondyle. An eminence above the condyle of a bone.

Epicoracoid. A bony element at the sternal end of the coracoid bone in some Amphibia.

Epidermis. The outer nonvascular skin layer.

Epididymis. The convoluted vasa efferentia at their origin in the testis.

Epiglottis. The lid that covers the entrance to the larynx.

Epimere. The dorsal division of the mesoderm wall.

Epinephrine. The secretion of the adrenal medulla.

Epiotic. On or above the ear.

Epiphysis. A small portion of bone separated by cartilage from the main body of bone during growth; the pineal body.

Epiploic. Pertaining to the great omentum.

Epipubic. Above the pubic bones.

Episternum. Above the sternum.

Epistropheus. The second cervical vertebra.

Epithalamus. The dorsal part of the diencephalon.

Epithelial bodies. The parathyroid glands.

Epithelium. The covering cellular layer of the skin and mucous membranes.

Epoöphoron. A vestigial mesonephric remnant associated with the ovary.

Erythrocyte. A red blood cell.

Esophagus. The part of the food tube extending from the pharynx to the stomach.

Estivate. To sleep through summer; to remain dormant in summer, in contrast to hibernate.

Estrogen. An ovarian hormone inducing estrus.

Estrone. An estrogenic steroid of ovarian origin.

Estrus. A cyclical period in female mammals, exclusive of human beings, marked by great sexual urge.

Eustachian tube. The tube connecting the middle ear with the pharynx.

Eusthenopteron. A genus of extinct fish.

Eutheria. True mammals.

Evagination. An outpocketing.

Excretion. Separation and removal of waste products.

Exoccipital bone. A division of the occipital bone lateral to the foramen magnum.

Exoskeleton. The external skeleton.

Facet. A small, oval articulating surface or face.

Falciform. A sickle-shaped ligament uniting the liver to the ventral body wall.

Fallopian tube. The anterior portion of the mammalian oviduct.

Falx. A fold.

Fascia. A connective tissue sheet covering muscles.

Fasciculus. A bundle.

Fauces. The passage connecting mouth and pharynx.

Fauna. The animal aggregate of a given region.

Feces. The excrement discharged from the bowels.

Fenestra. A window.

- Fertilization.** The union of sperm and ovum.
- Fetus.** The unborn mammalian offspring.
- Fibrin.** The thread-like, insoluble part of a blood clot.
- Fibrinogen.** A blood protein converted to fibrin by action of thrombin.
- Fibula.** The outer bone of the leg.
- Filoplume.** A hair-like feather.
- Fimbria.** The fringed margin of the oviduct.
- Fissure.** A cleft or a groove.
- Flagellum.** A whip-like process on certain cells.
- Flexion.** The act of bending.
- Flocculus.** A small, ventrally placed cerebellar lobe.
- Foliate papillae.** Taste buds on the lateral margin of the tongue.
- Follicle.** A small sac or gland.
- Fontanel.** Small unossified areas on the cranium of infants.
- Foramen.** An opening.
- Fornix.** An arch.
- Fossa.** A depression.
- Fovea centralis.** A small pit in the retina, the area of most acute vision.
- Frenulum.** A small fold or membrane that checks movement.
- Fundus.** The basal part of an organ farthest from its mouth.
- Funiculus.** The umbilical or spermatic cord.
- Furcula.** A small fork.
- Fusiform.** Spindle-shaped.
- Galea aponeurotica.** The fascial layer uniting parts of the scalp muscle.
- Ganglion.** A collection of nerve cell bodies.
- Ganoid.** Pertaining to a group of fishes with partly cartilaginous skeletons.
- Ganoin.** The outer, enamel-like layer of the ganoid scale.
- Gasserian ganglion.** The semilunar ganglion of the trigeminal nerve.
- Gastralia.** Abdominal ribs.
- Gastric.** Pertaining to the stomach.
- Gastrocele.** The cavity of the archenteron.
- Gastrula.** The embryonic stage succeeding the blastula in which ectoderm and endoderm have been differentiated.
- Gene.** A chromosomal unit, the carrier of hereditary factors.
- Geniculate.** Bent like a knee.
- Genital.** Pertaining to the reproductive organs.
- Genu.** The knee.
- Gerantic.** Pertaining to old age.
- Germinativum.** Relating to the deep layer of the epidermis.
- Gill rakers.** Comb-like array of branchial extensions at the base of a gill.
- Gizzard.** The muscular stomach of a bird.
- Gland.** An organ that elaborates a specific product.
- Glans penis.** The acorn-shaped head of the penis.
- Glenoid fossa.** The articulating cavity of the scapula.
- Glomerulus.** A small knot or tuft.
- Glottis.** The opening between the vocal cords.
- Gluteal.** Pertaining to the buttocks.
- Glycogen.** Animal starch, stored in the liver and in the muscles.
- Gnathostome.** Pertaining to vertebrates with jaws.
- Gonad.** The ovary or testis.

- Gonadotropin.** A hormone activating the male or female gonads.
- Graafian follicle.** The ovarian follicle.
- Gracilis.** A slender, elongate thigh muscle.
- Gubernaculum.** The cord attaching epididymis and scrotum and governing descent of the testis.
- Gullet.** The segment of the food tube between pharynx and stomach.
- Gynandromorphous.** Having both male and female characteristics.
- Gyrus.** A fold of the cerebral cortex.
- Habenula.** An area in the dorsal part of the thalamus.
- Habitat.** The natural home of an animal or plant.
- Hallux.** The great toe.
- Hamulus.** A small hook.
- Harderian glands.** Accessory lacrimal glands in animals with nictitating membranes.
- Hassall's corpuscles.** Small bodies in the thymus.
- Haversian canals.** Anastomosing channels in compact bone.
- Hemal.** Pertaining to the blood.
- Hemiazygous vein.** Venous trunk into which the left intercostal veins empty.
- Hemibranch.** A half gill.
- Hemipenes.** The trough-like copulatory organs in many reptiles.
- Hemopoietic.** Pertaining to the formation of blood.
- Henle's loop.** A loop in the nephron.
- Hepatic.** Pertaining to the liver.
- Hepatitis.** Inflammation of the liver.
- Herbivorous.** Pertaining to animals subsisting upon grasses and herbs.
- Heredity.** Transmission of characters from parents to offspring.
- Hermaphrodite.** A double-sexed individual.
- Heterocercal.** Having two unequal lobes in the tail fin.
- Heterodont.** A differentiated dentition.
- Hibernate.** To pass the winter in sleep.
- Hilum or hilus.** A depression where vessels or nerves enter.
- Hippocampus.** A submerged gyrus of the olfactory cerebral cortex.
- Histocyte.** A phagocytic cell of the reticuloendothelium.
- Holoblastic.** The condition in which the entire egg undergoes segmentation.
- Holobranch.** An entire gill.
- Holocrine.** Pertaining to glands in which the cells are disintegrated and used in the secretion.
- Homeostasis.** Uniformity or stability in the normal body states of an organism.
- Homocercal.** An outwardly symmetrical tail fin with asymmetry of the axial skeleton.
- Homodont.** Having one type of dentition throughout.
- Homology.** Structural similarity based upon common descent.
- Hormone.** A secretion of the ductless glands.
- Hyaline.** Glassy or translucent; a term denoting a type of cartilage.
- Hyapophysis.** A midventral process on the vertebral centrum.
- Hybrid.** Offspring resulting from the mating of two species.
- Hymen.** The membranous fold which closes the vaginal orifice.
- Hyoid arch.** The second visceral arch.
- Hyomandibula.** The dorsal segment of the hyoid arch.

- Hyostylic.** A type of jaw suspension in which the hyomandibula unites the jaw with the skull.
- Hypaxial.** Ventral to the lateral skeletogenous septum.
- Hypertension.** High blood pressure.
- Hyperthyroidism.** A condition produced by excessive secretion of the thyroid gland.
- Hypertrophy.** Overgrowth of a part.
- Hypobranchial.** Below the gills.
- Hypocone.** Posterior lingual cusp of an upper molar tooth.
- Hypoglossal.** Beneath the tongue; also, pertaining to the twelfth cranial nerve.
- Hypomere.** The ventral portion of the mesoderm.
- Hypophysis.** The pituitary body.
- Hypothalamus.** The ventral part of the diencephalon.
- Hypothesis.** A theoretical untested explanation for a phenomenon or a process.
- Hypothyroidism.** Underactivity of the thyroid gland.
- Hypselodont.** Pertaining to teeth with high crowns.
- Hypural.** Under the tail; pertaining to hemal arches extended into the tail.
- Ichthyopsida.** A category including fishes and amphibians.
- Ichthyopterygium.** Paired extremities of the fishes.
- Ileum.** The third and most posterior division of the small intestine.
- Ilium.** The dorsal part of the innominate bone.
- Imbrication.** An overlapping arrangement of parts.
- Incisor.** One of the cutting teeth in premaxilla and mandible.
- Incus.** Anvil-like; the middle ossicle of the ear.
- Infra-.** Prefix meaning "below."
- Infundibulum.** The funnel-like cavity leading to the pituitary gland.
- Inguinal.** Pertaining to the groin.
- Inner ear.** The portion of the ear including the bony and membranous labyrinth.
- Innominate.** Without name; term denoting the pelvic bone.
- Inscriptio tendinea.** Fibrous bands crossing the rectus abdominis muscle.
- Insulin.** The secretion of the islands of Langerhans.
- Integument.** The skin.
- Interarcuales.** Gill-arch muscles.
- Interdorsalia.** Vertebrae-forming segments of the sclerotome.
- Intergyrals.** Between cerebral convolutions.
- Interlobar.** Between the lobes.
- Internal capsule.** A nerve-fiber tract passing through the corpus striatum.
- Interparietal.** Between the parietal bones.
- Interrenal body.** A body in the fish kidney homologous with the adrenal cortex.
- Interstitial cells.** Cells outside the testicular tubules having hormonal functions.
- Intracellular.** Within a cell.
- Invagination.** A term denoting a pushing in or ingrowth of a part.
- In vitro.** Within glass.
- Involution.** A turning inward.
- Iris.** The pigmented tissue giving color to the eye posterior to the cornea.
- Ischium.** One of the parts of the innominate bone below the ilium.
- Islands of Langerhans.** Clusters of cells in the pancreas that secrete insulin.
- Isodont.** Having similar teeth.
- Iter.** A passage or opening.

Jacobson's organ. A specialized olfactory area in the nasal cavities.

Jejunum. Division of the intestine between duodenum and ileum.

Joint. An articulation.

Jugal point. The point at the masseteric and maxillary margins of the malar bone.

Jugate. Locked.

Jugular. Relating to the neck.

Juxtaposition. Denoting parts in apposition.

Karyochrome. A nerve cell in which the nucleus accepts stain and cytoplasm does not.

Karyon. The cell nucleus.

Keratin. An insoluble protein, the base of all horny tissue.

Kerato. A prefix designating horn or horn-like substances.

Keratotrichia. Fibrous, unjointed dermal fin rays.

Kidney. The urine-secreting organ.

Kinesiology. The study of muscular movements.

Kyphosis. Abnormal curvature of the back; humpback.

Labia. The plural of labium; lips.

Labrum. A fibrous ring about a socket which increases its depth.

Labyrinth. Intercommunicating channels, particularly the canals of the inner ear.

Lacrimal. Pertaining to tears or to the tear gland.

Lacteals. The intestinal lymphatic capillaries.

Lacuna. A small hollow; a depression.

Lamella. A thin plate.

Lamina. A flat plate.

Lancet. A small, two-edged surgical knife.

Langugo. Delicate hair on the body of a fetus.

Laparotomy. A surgical incision through the flank.

Laryngeal. Pertaining to the voice box at the head of the trachea.

Lateral line. A line on the sides of a fish, carrying sensory endings.

Lemniscus. A tract of sensory nerve fibers from the medulla to the thalamus.

Lentiform. Like a lens in shape.

Leucocyte. A white blood cell.

Levator. A muscle that lifts a part.

Lienal. Pertaining to the spleen.

Ligament. A fibrous tissue or bands that tie bones together or support visceral organs.

Ligature. A thread for tying, particularly in surgery.

Linea. A line.

Lingual. Pertaining to the tongue.

Lipase. A fat-splitting enzyme.

Lipid. Pertaining to fats and steroids.

Lobule. A small lobe.

Lophodont. A type of molar dentition with cross ridges.

Lumbar. Pertaining to the region of the loins.

Lumbrical. Worm-like; a muscle in the hand.

Lumen. The channel or hollow center in a tube or organ.

Lunate. Crescent-shaped.

Lunula. Crescent-shaped white area at the base of a nail.

Luteal. Pertaining to the corpus luteum.

- Lymph.** The fluid in the lymphatic vessels.
- Lymph hearts.** Contractile lymph sacs in amphibians.
- Lymphocyte.** A type of white blood cell.
- Macrocyte.** A giant blood cell or lymphocyte.
- Macrophage.** Large, wandering phagocyte.
- Macula.** A spot.
- Malar.** Relating to the cheek bone.
- Malleolus.** A small hammer; rounded projections at the ankle.
- Malleus.** A hammer; one of the ear ossicles.
- Malpighian corpuscle.** The blood vessel knot, together with Bowman's capsule, at the origin of the uriniferous tubule of the kidney.
- Mammae.** The mammary glands.
- Mamillary bodies.** Two small masses of gray substance on the base of the brain.
- Mandible.** The lower jaw.
- Mantle.** The cerebral cortex.
- Manubrium.** A handle.
- Manus.** The hand.
- Margo.** A border.
- Marine.** Pertaining to the sea.
- Marsupial.** One of a class of animals with abdominal pouches.
- Masseter.** A muscle that elevates the lower jaw.
- Mastoid.** A process of the temporal bone.
- Matrix.** The uterus; intercellular substance.
- Maxilla.** The upper jaw.
- Maximus.** The greatest.
- Meatus.** A channel or passage.
- Meckel's cartilage.** Cartilage forming the lower jaw of cartilaginous fishes.
- Mediastinum.** The septum enclosing the heart and separating the two pleural cavities.
- Medius.** The middle.
- Medulla.** The marrow.
- Medullated.** Covered by a sheath.
- Megaloblast.** A large, primitive red blood cell.
- Meibomian glands.** Sebaceous glands of the eyelids.
- Melanin.** The dark pigment of the skin.
- Meninx.** Singular of meninges; the membrane enveloping brain and spinal cord.
- Menisci.** Crescent-shaped interarticular cartilages in the knee joint.
- Mental.** Pertaining to the mind or to the chin.
- Meristic.** Symmetrical.
- Meroblastic.** Relating to cleavage involving only a part of the cell.
- Mesoderm.** The middle germ layer.
- Mesogaster.** The midgut; mesentery that attaches stomach to body wall.
- Mesomere.** The nephrotome.
- Mesonephros.** The functional kidney of fishes and amphibians.
- Mesopterygium.** The middle cartilage in the base of the elasmobranch fin.
- Mesorchium.** The mesentery supporting the testis in the body cavity.
- Mesorectum.** The mesentery supporting the rectum.
- Mesothelium.** The mesodermal lining of the body cavity.
- Mesovarium.** The mesentery supporting the ovary.

- Metabolism.** The sum of chemical changes in living organisms.
- Metacarpal.** Pertaining to the wrist bones.
- Metacone.** The posterior-lateral cusp of the mammalian upper molar.
- Metacromion.** A process on the spine of the scapula.
- Metamerism.** Segmentation of body parts.
- Metamorphosis.** Transformation.
- Metanephros.** The kidney of reptiles, birds, mammals.
- Metapleural.** Pertaining to ventrolateral folds in *Amphioxus*.
- Metapterygium.** A basal cartilage in the elasmobranch pectoral fin.
- Metastasis.** The passage of infection or disease from one part of the body to another.
- Metatarsal.** Pertaining to the foot bones between the tarsus and phalanges.
- Metathrombin.** Substance developed from thrombin upon exposure to air.
- Metazoan.** Any many-celled animal.
- Metencephalon.** The hindbrain.
- Micron.** The one-thousandth division of a millimeter.
- Midbrain.** The mesencephalon.
- Minimus.** The smallest.
- Minor.** The lesser or smaller.
- Mitosis.** A process of cell division.
- Mitral.** From miter; the left atrioventricular heart valves.
- Molar.** Pertaining to grinding teeth.
- Molt.** A shedding.
- Monocyte.** A large white blood cell with indented nucleus.
- Monoecious.** Having both sexes represented in one organism.
- Monophyodont.** Having single set of teeth, none of which are later replaced by others.
- Monotreme.** Pertaining to the egg-laying mammals.
- Morphology.** The science of the form and structure of plants and animals.
- Morula.** Cleavage stage of the egg, resembling the mulberry.
- Mucosa.** The mucous membrane lining the digestive tract.
- Müllerian duct.** The oviduct.
- Multangular.** Pertaining to two of the bones in the distal row of wristbones.
- Multifidus.** Split into many parts; a group of small back muscles.
- Multituberculate.** Having many tubercles or cusps.
- Muscularis mucosae.** A layer of smooth muscle fibers in the intestinal mucosa.
- Mutation.** A heritable change due to permanent alteration of chromosomes in the germ cells.
- Myelencephalon.** The medulla oblongata.
- Myelin sheath.** The fat-like covering of nerve fibers.
- Myelocyte.** A typical red bone marrow cell.
- Myocomma.** The division between two myotomes.
- Myomere.** A muscular segment.
- Myoseptum.** The connective tissue septum between adjacent myotomes.
- Myxedema.** A wasting disease caused by underfunctioning of the thyroid gland in the adult.
- Myxine.** The hagfish of the class *Cyclostomata*.
- Nares.** The nostrils.
- Narism.** A dwarfed state.
- Nasal conchae.** The shell-shaped, curved, hollow bony plates in the nasal fossa.

- Nasoturbinal.** Denoting the nasal conchae.
- Natural selection.** The unconsciously controlled mating of plants or animals whereby certain species characteristics are maintained, augmented, or diminished.
- Navel.** The abdominal scar left after separation of the umbilical cord.
- Navicular.** Boat-shaped; pertaining to one of the wrist and ankle bones.
- Nephridium.** The embryonic excretory organ.
- Nephrosotome.** The opening of the nephridium in the celom.
- Nephrotome.** One of the divisions of the embryonic myotome which develops into the urogenital organs.
- Neural.** Relating to the nervous system.
- Neurilemma.** The outer covering of the myelin nerve sheath.
- Neurite.** The nerve axon.
- Neurocele.** The brain ventricles, together with the central canal of the cord.
- Neurocranium.** The part of the skull which houses the brain.
- Neuroglia.** The cells supporting the nervous tissue.
- Neuromast.** A group of sensory cells combined as a sense organ.
- Neuron.** A nerve cell, together with its processes.
- Neuropile.** Fine unmyelinated fibers forming a network in the central nervous system, presumably capable of diffusing nervous impulses.
- Neuropore.** The anterior open end of the embryonic brain.
- Nictitating membrane.** The third eyelid of many animals.
- Nissl body.** A group of granules with basic staining reaction in the nerve cells.
- Nocturnal.** Pertaining to activity in the night.
- Nodes of Ranvier.** Constrictions on medullated nerve fibers.
- Nodosal.** Pertaining to projections, specifically to a ganglion of the vagus nerve.
- Nomogenesis.** A theory according to which evolution is predetermined and not affected by chance.
- Notochord.** The axial supporting column of the Protochordata.
- Nuchal.** Pertaining to the back of the neck.
- Nucleolus.** A small round body within the nucleus.
- Nucleus.** The spherical body within the cell and vital to its existence; the center of origin of certain nerves.
- Nystagmus.** A rapid involuntary movement of the eyeball.
- Obesity.** Excessive accumulation of fat.
- Obturator foramen.** The opening between pubis and ischium.
- Occipital.** Pertaining to the skull region about the foramen magnum.
- Occlusion.** Closure; the meeting of the teeth when the jaws are closed.
- Ocular.** Relating to the eye.
- Odontoid process.** The tooth-like process of the second vertebra.
- Olecranon.** The curved process at the proximal end of the ulna.
- Olfactory.** Pertaining to smell or to the smelling organ.
- Olivary bodies.** Small oval prominences lateral to the pyramids of the medulla.
- Oma.** A suffix or termination indicating a pathologic condition.
- Omasum.** The third division of the ruminant stomach.
- Omentum.** The sac formed by folding of the peritoneum covering stomach and intestine in the adult mammal.
- Omnivorous.** Pertaining to food habits, specifically utilization of food of every kind.

- Omphalomesenteric.** Relating to the umbilicus and the mesentery.
- Ontogeny.** The development of the individual.
- Opercular bone.** A covering bone over the gill region of fishes.
- Ophidia.** An order of reptiles including the snakes.
- Ophthalmic.** Relating to the eye.
- Opisthonephros.** An extension of the mesonephros resembling the metanephros, occurring in certain anamniotes.
- Opisthotic.** Pertaining to skeletal elements posterior to the ear in fishes.
- Optic.** Pertaining to the eye.
- Oral.** Relating to the mouth.
- Ora serrata.** The jagged margin of the retina where it meets the ciliary body.
- Orbit.** The eye socket.
- Orchis.** The testis.
- Organism.** The combined and organized interdependent parts resulting in an individual plant or animal.
- Organ of Corti.** The hearing apparatus within the cochlea.
- Os.** The Latin term for mouth and for bone.
- Os coxae.** The innominate bone.
- Osculum.** Any small opening.
- Osmosis.** The passage of a solvent through a semipermeable membrane.
- Os priapi.** The bone in the penis of certain mammals.
- Osteoblast.** A bone-forming cell.
- Osteoclast.** A bone-absorbing cell.
- Osteogenesis.** The development of bone.
- Ostium tubae.** The opening of the fallopian tube in the uterus.
- Otic.** Relating to the ear.
- Otolith.** A calcium carbonate body in the membranous labyrinth of the ear.
- Ovary.** The female sex gland in which eggs are formed.
- Oviparous.** Pertaining to egg laying.
- Ovulation.** The process of egg discharge; the production of eggs with a shell or covering that are hatched within the body.
- Ovum.** The egg.
- Oxytocin.** A product from the posterior lobe of the pituitary gland which causes uterine contraction.
- Pacemaker of the heart.** The sinuauricular node.
- Pachyderma.** An abnormally thick skin, also applied to the elephant.
- Pacini's corpuscles.** A type of tactile corpuscle.
- Palatoquadrate.** Pertaining to the palatine and quadrate cartilage or bone.
- Paleontology.** The study of fossil life.
- Paleozoic.** The interval from the Cambrian to the Permian periods inclusive.
- Pallium.** The cortex and white matter of the cerebrum.
- Palpebra.** The eyelid.
- Papilla.** A small elevation.
- Parabiosis.** The natural or artificial joining of two individuals.
- Parachordal.** Pertaining to cartilages parallel with the anterior end of the notochord.
- Parahormone.** A secretion acting like a hormone, but not a true hormone.
- Paraphysis.** An outgrowth from the roof of the telencephalon.
- Parasympathetic.** Pertaining to the craniosacral division of the autonomic nervous system.

- Parathormone.** The secretion of the parathyroid glands.
- Parathyroid glands.** Endocrine glands in proximity to the thyroid glands.
- Paraxonic.** Pertaining to collateral branches of axons.
- Parietal organ.** An epiphyseal development from the roof of the diencephalon.
- Paroöphoron.** A vestige of the mesonephros in the broad ligament of mammals.
- Pecten.** A comb-like body in the vitreous humour of reptiles and birds.
- Pectinate.** Like crest or comb in shape.
- Pectoral.** Pertaining to the breast or chest.
- Pectus.** The breast of a bird.
- Peduncle.** A stem or supporting structure.
- Pelagic.** Pertaining to the surface of the ocean.
- Pellucid.** Pertaining to translucent tissue.
- Pelvis.** The combined innominates and sacrum forming a basin-like support.
- Penis.** The male copulatory organ.
- Penis bone.** A bone in the penis of certain mammals.
- Pentadactyl.** Having five fingers or toes.
- Pepsin.** A digestive ferment.
- Peri-.** Prefix meaning "around."
- Pericardial cavity.** The space in which the heart lies.
- Pericardium.** The sac surrounding the heart.
- Perilymph.** The fluid immediately outside the internal membranous ear.
- Perimysium.** The delicate connective tissue sheath about muscle fibers.
- Perineum.** The region or space about the anus and genitourinary orifices.
- Periosteum.** The fibrous membrane surrounding bone.
- Peripheral.** Toward the surface or boundary.
- Peristalsis.** The contraction wave of the intestine.
- Perithelium.** The fibers that surround small blood vessels and capillaries.
- Peritoneum.** The lining membrane of the abdominal cavity, which also encloses the visceral organs.
- Petrosa.** A division of the temporal bone.
- Peyer's patches.** Lymphatic glands in the ileum of mammals.
- Phagocyte.** A cell that ingests bacteria and other substances.
- Phalanx.** A bone of the finger or toe.
- Phallic.** Pertaining to the penis.
- Pharynx.** The sac between mouth, nares, and esophagus.
- Phlegm.** Mucus secretion from nose and throat.
- Photon.** A light particle of cosmic energy.
- Photophore.** A luminous cell or organ.
- Photosynthesis.** The process of chemical combination of carbon dioxide, water, and chlorophyll by the action of light.
- Phrenic.** Pertaining to the diaphragm.
- Phylogeny.** The racial history of an animal or plant.
- Phylum.** A primary division of the plant or animal kingdom.
- Physoclistous.** Pertaining to an air bladder without an orifice.
- Physostomous.** Pertaining to an air bladder with an opening.
- Phytogenesis.** Relating to the origin of plants.
- Pigeon's milk.** The crop secretion of certain birds.
- Pigment.** Coloring matter.
- Pineal body.** An outgrowth from the roof of the diencephalon.
- Piriformis.** A pear-shaped mammalian muscle.

- Pisces.** The class of fishes.
- Pisiform.** Pea-shaped; one of the wrist bones.
- Pituitary.** One of the cells of the pars nervosa of the pituitary gland.
- Pituitrin.** A secretion of the posterior lobe of the pituitary gland, which causes smooth muscle contraction.
- Placenta.** The organ within the uterus which establishes a nutrient connection between mother and fetus.
- Placentalia.** A division of animals having a placenta.
- Placode.** An ectodermal plate forming the primordium of an organ.
- Placoid.** Pertaining to a type of scale present in elasmobranchs.
- Plantar.** Relating to the sole of the foot.
- Plantigrade.** Relating to a division of animals walking on the sole of the foot.
- Plasma.** The fluid part of the blood.
- Plastron.** The ventral exoskeletal plate in turtles.
- Plasmolysis.** The shrinking of a cell, owing to loss of water, when placed in a hypertonic solution.
- Platybasic.** Pertaining to a skull with a broad, flat base.
- Platysma.** A superficial muscle sheet of the neck.
- Plectrum.** The malleus; also the styloid process of the mastoid bone.
- Pleura.** The serous membrane surrounding the lungs.
- Pleurodont.** Relating to teeth that are fused with the inner edges of the jaws, as in some reptiles.
- Pleuroperitoneal.** Pertaining to the body space or its lining in animals without a diaphragm.
- Plexus.** A network of blood vessels or nerves.
- Plicae circulares.** Circular folds in the intestinal lining.
- Plumule.** A small feather.
- Pneumatic.** Pertaining to air and to breathing.
- Pneumogastric.** Relating to lung and stomach, also to the vagus nerve.
- Pneumothorax.** Accumulation of air or other gases in the pleural cavity.
- Pollex.** The thumb.
- Polyphyodont.** Indefinite tooth succession.
- Pons.** A bridge of transverse nerve fibers below the medulla oblongata, uniting it with the cerebrum and cerebellum.
- Popliteal space.** The posterior surface of the knee.
- Portal system.** A system of veins to the liver, and to the kidney in some fishes, amphibians, and reptiles, interrupted by capillaries in these organs. The capillaries reunite into veins that convey blood to the heart.
- Post-.** A prefix meaning "behind" or "after."
- Pre-.** A prefix meaning "in front of" or "before."
- Prehensile.** Adapted for grasping and seizing.
- Premolar bicuspid.** Teeth in front of the molars.
- Prepuce.** The foreskin of the penis.
- Primate.** An animal order including monkeys, apes, and man.
- Primordial.** Pertaining to the early origin of parts or cells.
- Primordium.** The anlage of a part.
- Pro-.** A prefix meaning "before."
- Process.** An extension or an outgrowth.
- Proctodeum.** One of the divisions of the cloaca.

- Progesterin.** An endocrine secretion from the corpus luteum of the ovary.
- Pronation.** Movement of a hand to a palms-downward position.
- Pronephros.** The first chordate urinary organ.
- Propterygium.** The first basal cartilage of the elasmobranch pectoral fin.
- Prosencephalon.** The most anterior embryonic division of the brain.
- Prostate gland.** A gland associated with the male membranous urethra and the neck of the bladder.
- Protein.** A nitrogenous compound present in animal tissue.
- Protocone.** The medial cusp of an upper molar tooth.
- Proventriculus.** The glandular stomach of birds.
- Proximal.** Nearest to the point of origin.
- Psalterium.** The third stomach of ruminants.
- Pseudo-** A prefix meaning "false".
- Pterodactyl.** An extinct flying reptile.
- Pterygium.** A little wing; used in connection with fin and bone terminology.
- Ptyalin.** A digestive ferment in saliva.
- Puberty.** The period of functional ripening of the generative organs in man.
- Pubis.** The anterior of the three bones forming the innominate.
- Pudendum.** The external female genital organs.
- Pulp.** Soft animal or plant tissue.
- Pupil.** The opening in the center of the iris.
- Purkinje cells.** Many-branched neurons in the cerebellar cortex.
- Pygal.** Pertaining to the tail.
- Pylorus.** The distal end of the stomach (literally, gate keeper).
- Pyramid.** A cone-shaped eminence; designates various masses associated with a number of organs, *e.g.*, renal, medullary, vermis, and vestibule.
- Pyro-** A prefix denoting heat or fire.
- Quadrangle.** Four-sided.
- Quadriceps.** Having four heads.
- Quadrigenina.** In four parts.
- Quantum.** The unit of energy.
- Race.** A breed of animals; an ethnic division of mankind.
- Rachis.** The distal end of a feather shaft; the backbone.
- Radial.** Pertaining to cartilages distal to the basal in the pectoral appendage of elasmobranchs; one of the arteries in the forearm.
- Radial symmetry.** Symmetry based on a wheel-shaped body pattern.
- Radix.** A root.
- Ramus.** A branch of a vessel, nerve, or bone.
- Raphe.** A seam or union marking the midline union of muscles or tendons.
- Rasores.** A division of birds, including the common fowl, which scratch the earth for food.
- Ratite.** Pertaining to nonflying birds without a keel.
- Ray.** A delicate, rod-like supporting structure, or the arrangement of tubes as in the kidney.
- Receptor.** A sensory nerve cell.
- Recessus.** A cavity or empty space.
- Rectum.** The distal fraction of the large intestine.
- Reflex.** An involuntary action produced by nerve stimulation.
- Reflex arc.** The nerve pathways concerned in a reflex action.
- Regeneration.** Renewal or repair of tissue.

- Remiges.** The quill feathers of the bird wing.
- Renal.** Pertaining to the kidneys.
- Renal corpuscle.** The tuft of blood vessels and the surrounding expanded part of the uriniferous tubule.
- Renal portal system.** The system of veins and capillaries returning blood to the heart via the caudal and renal veins.
- Reproduction.** Production of offspring.
- Rete.** A network of blood vessels, nerve fibers, or tubules.
- Rete mirabile.** A network of blood vessels.
- Rete testis.** The fine network of tubules uniting the seminiferous tubules and the efferent duct of the testis.
- Reticulum.** A net-like arrangement of fibers.
- Retina.** The innermost and sensitive nervous structure of the eye, consisting of seven layers including the rods and cones.
- Retrices.** Feathers of a type that project backward
- Retro-.** A prefix meaning "to recede" or "to go backward."
- Rhinal.** Pertaining to the olfactory organ.
- Rhombo-.** A prefix denoting a parallelogram or kite-shaped figure.
- Rhynchocephalia.** An order of lizards.
- Rodent.** An order of mammals.
- Rods and cones.** The light-sensitive layer of the retina.
- Rostrum.** A beak-like structure or process.
- Round ligament.** A ligament extending from the uterus to the labium majus.
- Rudimentary.** Vestigial or partly developed.
- Rumen.** The first division of the ruminant stomach.
- Ruminant.** A cud-chewing animal with a four-compartment stomach.
- Sacculus.** One of the divisions of the vesicle of the inner ear.
- Sacral.** Pertaining to the fused vertebrae forming the sacrum.
- Sagittal.** Arrow-like; pertaining to a dorsoventral or anteroposterior section.
- Salivary.** Relating to the secretion of the digestive glands associated with the mouth.
- Saphenous.** Pertaining to a large vein in the leg that opens into the femoral vein.
- Sarcolemma.** The membrane surrounding a muscle fiber.
- Sarcomere.** A transverse segment in a muscular fibril.
- Sarcoplasm.** The matter in which the muscle fibrils are enclosed.
- Sauropsida.** A group of vertebrates including the birds and the reptiles.
- Scala media.** The cochlear canal of the inner ear.
- Scala tympani.** One of the canals of the cochlea.
- Scala vestibuli.** One of the divisions of the spiral cochlear canal.
- Scalene.** Pertaining to one of the irregular three-sided muscles attached to the upper ribs and neck vertebrae.
- Scapula.** The flat, triangular shoulder bone.
- Sciatic.** Relating to the ischium; specifically, the great nerve trunk emerging below the ischium.
- Sclera.** The white connective tissue or cartilaginous outer covering of the eyeball.
- Sclerotome.** The mesodermal tissue in the embryo responsible for skeletal formation.
- Scrotal sac.** The pouch which contains the testes.

- Scute.** The shield-shaped or scale-like bony plate.
- Sebaceous gland.** A gland secreting an oily substance.
- Sebum.** The secretion of the sebaceous gland.
- Secodont.** Pertaining to dentition adapted for cutting.
- Secretin.** A hormone from the duodenal mucosa which induces pancreatic secretion.
- Sedentary.** Stationary.
- Segmental.** Pertaining to serially repeated structures.
- Selenodont.** Molar dentition with crescentic ridges on the crown.
- Sella turcica.** The saddle-shaped depression in the floor of the skull in which lies the pituitary gland.
- Semen.** The product, including sperm and secretions of the testes, discharged in coitus.
- Semilunar.** Half-moon-shaped.
- Seminal.** Relating to the secretion of the testes.
- Seminal vesicle.** A convoluted outgrowth of the ductus deferens near the base of the bladder.
- Seminiferous.** Pertaining to the secretion of sperm.
- Septum.** A wall or partition.
- Serosa.** A membrane secreting a watery fluid.
- Serous.** Relating to serum.
- Serratus.** With jagged or tooth-like edges.
- Serum.** The clear liquid fraction of the blood.
- Sesamoid.** Shaped like the seed of the sesame plant; small bones developed in certain tendons.
- Sessile.** Fixed by a broad attachment or base.
- Sibling.** One of two or more progeny of the same parents.
- Sigmoid.** S-shaped; the lower end of the human colon.
- Sinus.** A hollow space.
- Sinus venosus.** One of the chambers of the heart, well developed in the anamniotes.
- Skeletogenous.** Pertaining to skeletal-forming tissue.
- Solar.** Pertaining to the sun.
- Soleus.** One of the flat muscles of the shank.
- Somatic.** Relating to the body framework, as distinguished from splanchnic, which refers to the viscera.
- Somatopleure.** The parietal mesoderm and covering ectoderm.
- Somite.** A mesodermal body segment.
- Space.** A cavity or a given area of the body.
- Species.** A primary classification division below a genus.
- Sperm.** The male germ cells.
- Spermatozoan.** Pertaining to the mature male germ cell.
- Sphenodon.** A genus of reptiles of the order Rhynchocephalia.
- Sphenoid.** The wedge-shaped bone at the base of the skull.
- Sphincter.** An annular muscle enclosing and constricting an opening.
- Spinal accessory.** Pertaining to the eleventh cranial nerve.
- Spine.** A pointed process of bone; the backbone.
- Spiracle.** A rounded opening leading from the roof of the mouth to the exterior in many fishes.

- Spiral valve.** A spirally attached, absorptive fold in the intestine of elasmobranchs and some other fishes.
- Spleen.** A ductless gland that destroys red blood cells in the adult.
- Squame.** A scale.
- Squamous.** Pertaining to scale-like cells.
- Stapedius.** A small muscle of the inner ear.
- Stapes.** The inner, stirrup-shaped ossicle of the ear.
- Stegocephalia.** An extinct subclass of amphibians.
- Sternalia.** The segments of the sternum.
- Sterno-.** A prefix denoting the breast bone.
- Stomodeum.** The oral opening of the embryonic alimentary canal.
- Stratified.** In layers.
- Stratum.** A single layer or plane.
- Striatum.** The grooved body in the brain called corpus striatum.
- Stroma.** The connective tissue that forms the framework of an organ.
- Stylo-.** A prefix denoting a pointed, pen-like process.
- Sub-.** A prefix meaning "beneath."
- Subclavian.** Pertaining to structures underneath or below the clavicle.
- Sublingual.** Below the tongue.
- Submaxillary.** Underneath the maxilla.
- Submental.** Below the chin.
- Submucosa.** The layer below the mucosa.
- Subscapular.** Underneath the scapula.
- Succus entericus.** The intestinal secretions.
- Sudoriparous glands.** The sweat glands.
- Sulcus.** A furrow; a fissure in the brain.
- Supination.** Turning the palm of the hand upward.
- Supine.** Lying on the back.
- Supra-.** A prefix meaning "above."
- Suspensory ligament.** A ligament that holds up a part.
- Suture.** The junction of neighboring bones; a surgical stitch.
- Symphysis.** A junction of adjacent bones.
- Syn-.** A prefix denoting a union.
- Synapse.** The region where the axon of one nerve cell forms a contact with a dendrite of another.
- Synarthrosis.** An immovable suture or joint.
- Syndactylus.** A person having a condition in which fingers or toes are fused.
- Syndrome.** A group of symptoms occurring together.
- Synergist.** A muscle or other organ acting cooperatively with another similar organ.
- Synovia.** The fluid secreted in a joint cavity.
- Synsacrum.** The fused lumbar, sacral, and caudal vertebrae that augment and support the pelvic girdle in birds.
- Syrinx.** The specialized sound-producing mechanism at the tracheal bifurcation in birds.
- System.** A group of organs acting together to produce a common function.
- Systemic.** Pertaining to the body as a whole.
- Systole.** The contraction of the heart.
- Tactual.** Pertaining to the touch.

- Taenia.** Bands of longitudinal muscle fibers along the colon.
- Talus.** A bone in the proximal row of ankle bones.
- Tapetum.** The pigmented layer of the retina.
- Tarsal gland.** A sebaceous gland in the eyelid.
- Tarsus.** The ankle.
- Tectorium.** A membrane in the organ of Corti.
- Tectum.** The roof of the mesencephalon including the corpora quadrigemina.
- Tegmen.** A covering.
- Telencephalon.** The anterior division of the forebrain.
- Teleosts.** An order of bony fishes.
- Tendon.** The tough connective tissue ends of a muscle by which it is attached to the skeleton.
- Tentorium.** The dural partition between the cerebellum and the cerebrum.
- Teres.** Cyclindrical muscles of the shoulder.
- Terminal.** Relating to the end of a structure.
- Terrestrial.** Pertaining to earth-dwelling animals as distinguished from aquatic.
- Testis.** The male generative organ.
- Testosterone.** A male sex hormone liberated in the testes, affecting the secondary male characteristics.
- Tetany.** A steady tonic muscle spasm.
- Tetrapod.** A vertebrate with four appendages.
- Thalamus.** Gray nerve mass in the diencephalon surrounding the third ventricle.
- Thecodont.** A type of dentition embedded in sockets in the jaws.
- Thorax.** The body division between the abdomen and the neck.
- Thymus gland.** A ductless gland in the anterior region of the neck and throat.
- Thyroid.** Shield-shaped; pertaining to the laryngeal cartilage, the gland, and other structures in proximity to the cartilage.
- Thyrotropin.** A hormone secreted by the anterior lobe of the pituitary gland that activates the thyroid gland.
- Thyroxin.** The crystalline iodine-containing agent isolated from the thyroid gland.
- Tibia.** The shin bone.
- Tigroid.** Spotted; pertaining to deeply staining granules in nerve cells.
- Tissue.** An aggregation of similar cells carrying on a particular function.
- Trabecula.** A column, bundle, or network of cells forming part of the supporting stroma of an organ.
- Trachea.** That part of the respiratory tube extending from the larynx to the bronchi.
- Trapezoid.** Table-shaped; pertaining to structures approaching the shape of a trapezium.
- Trema-.** A combining form, denoting an opening.
- Tri-.** A prefix indicating three parts.
- Triceps.** With three heads.
- Tricuspid valve.** A valve with three pockets.
- Triquetral.** A triangular bone in the proximal row of wrist bones.
- Trochanter.** Either of the two processes on the proximal part of the femur.
- Trochlea.** A pulley-shaped part; the medial articulation of the distal end of the humerus.
- Tuber.** An enlargement or swelling; rounded, projecting skeletal structures.

- Tunicate.** A member of the subphylum Urochordata.
- Turbinal.** Top-shaped; pertaining to the nasal conchae.
- Tympanic membrane.** The membrane separating the middle from the outer ear.
- Tympanum.** The middle ear.
- Ulna.** The bone in the forearm on the side of the fifth finger.
- Ultimobranchial bodies.** Gill-pouch-derived glands fused with the thyroid glands in man, presumably with endocrine function.
- Umbilical cord.** The cord linking mother and fetus in viviparous animals.
- Umbilicus.** The navel.
- Uncinate.** Relating to a hook-shaped process.
- Unguiculate.** Having claws as distinguished from hoofs.
- Unguis.** A nail, hoof, or claw.
- Ungulate.** A hoofed animal.
- Urea.** The nitrogenous constituent of urine.
- Ureter.** The tube extending from the kidney to the bladder.
- Urethra.** The tube extending from the urinary bladder to the outside.
- Uro-.** A prefix denoting a relation to urine and also to tail; e.g. urinary tract; Urodeles, or tailed amphibia.
- Urodele.** An order of amphibians.
- Urogenital.** Pertaining to the excretory and reproductive organs.
- Uterus.** The womb.
- Utricle.** A small sac or bag; one of the compartments in the inner ear.
- Uvula.** The small pendent body attached to the roof of the soft palate.
- Vacuole.** A small space in the protoplasm of a cell.
- Vagina.** The sheath-like canal extending from the cervix of the uterus to the labia.
- Vagus.** Wanderer; the tenth cranial nerve.
- Vallate.** Cup-shaped; pertaining to taste bodies of that shape.
- Valve.** A fold in a vessel or organ that prevents backflow of the contents.
- Vane.** The expanded part of a feather.
- Vas (pl. Vasa).** A vessel or duct.
- Vascular.** Pertaining to the blood vessels.
- Vasomotor.** Relating to nerves acting upon the blood vessels.
- Vastus.** Large; e.g., vastus lateralis muscle.
- Vein.** A vessel conveying blood to the heart.
- Velum.** A covering or veil.
- Vena.** A vein.
- Vent.** An opening; generally the anus.
- Venous.** Pertaining to the veins.
- Venter.** The stomach or belly.
- Ventral.** The abdominal side.
- Ventricle.** A small cavity, especially the two lower heart cavities and those in the brain.
- Vermiform.** Worm-shaped.
- Vermis.** Latin for "worm"; designates the worm-like median lobe of the cerebellum.
- Vertebra.** One of the skeletal segments of the spinal column.
- Vesicle.** A small sac or bladder.
- Vestibule.** An antechamber or entrance to a canal or cavity.

- Vestigial.** Pertaining to a rudimentary part.
- Viable.** Capable of living.
- Vibrissae.** Hairs able to transmit sensory impulses, located in the nostrils and on the face.
- Villus.** A small, finger-like projection or tuft.
- Virus.** A living agent capable of causing disease, usually ultramicroscopic.
- Viscera.** Plural of viscus.
- Viscus.** Any organ in the body cavity.
- Visual purple.** A pigment in the retina aiding in night vision.
- Vitelline.** Pertaining to the yolk of an ovum.
- Vitreous.** Glassy; pertaining especially to the fluid in the chamber bounded by the retina and lens of the eye.
- Viviparous.** Bringing forth young alive, as distinguished from oviparous, or egg-laying.
- Vivisection.** Any operation upon a living animal.
- Vomer.** The plowshare bone in the floor of the nasal septum.
- Vulva.** The external female generative organs.
- Wax, ear-.** The ceruminous secretion in the outer ear.
- Wharton's duct.** The duct of the submaxillary gland.
- Winslow's foramen.** The opening from the hepatoduodenal ligament into the omentum behind the portal fissure of the liver.
- Wolffian ducts.** The mesonephric ducts.
- Womb.** The uterus.
- Xiphi-.** A prefix meaning "sword-shaped."
- Xiphisternum.** The pointed posterior segment at the lower end of the sternum.
- Yolk.** The nutrient part of an egg.
- Zoo-.** A combining term denoting animal.
- Zoogeography.** The study of animal distribution.
- Zygo-.** A combining term denoting a yoke or pair.
- Zygote.** The cell formed by conjugation of two gametes.

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